

Studies on the Banana

An investigation of the Floral Morphology and
Cytology of certain types of the Genus *Musa* L.

By

Philip R. White

DISSERTATION

submitted to the Board of University Studies
of the Johns Hopkins University in partial
fulfillment of the requirements for the degree
of Doctor of Philosophy

Verlagsbuchhandlung Julius Springer in Berlin

1928



PART I.

Introductory.

The banana (which in the broad sense, includes all of the forty odd species and hundreds of varieties of the genus *Musa* L.) is one of the oldest and most important of all the food plants of the human race. Until quite recently, however, it has received very little attention from the world of science. In spite of the general anatomical papers of WITTMACK (76) and GREVE (25), the cytological papers of TISCHLER (70, 71) and D'ANGREMOND (1, 2), studies in the anatomy and germination of seeds by CATIN (16, 17) and the taxonomic studies by SCHUMANN (60), FAWCETT (22), BAKER (4), QUISUMBING (51) et. al., there is relatively little detailed information available. Like most tropical plants, the banana is not easily available for scientific studies without the aid of the growers.

Recently their interest in such work has increased on account of the so-called "Panama disease" (a fusarium infection). It has become desirable to find some means of combatting this disease and the present investigation was primarily undertaken with this problem in mind.

It has been conducted with the aid of a grant from the United Fruit Company of Boston, to whom, in the persons of Mr. G. P. CHITTENDEN, General Manager and Dr. JOHN R. JOHNSTON, Director of Agricultural Research, my thanks are especially due².

In dealing with such a situation there are in the main, two methods of attack: (1) to rid the host and its environment of the pathogenic

¹ Botanical Contribution from the Johns Hopkins University, Nr. 96.

² The work here presented was begun during the summer of 1926 while the writer was a member of the Botanical Expedition of the Johns Hopkins University to Jamaica, and was continued during the following two winters in the Botanical Laboratories of Johns Hopkins University, and during the summer of 1927 on the United Fruit Company's experimental plantations at Almirante, Panama. I am especially indebted to Professor D. S. JOHNSON for his encouragement and advice throughout the conduct of the work.

organism, that is to remove the source of infection, and (2) to render the host resistant to the infecting organism. Since *Fusarium cubense* E. F. SMITH (BRANDES, 12) the organism causing "Panama disease" enters the host from the soil, where it may be very widespread and where it is easily distributed by the surface water so abundant in the tropics at some seasons, it is out of the question to completely sterilize the environment. The virulence of the disease has been found to be, to some extent, dependent on soil conditions, but it is seldom possible to obtain the optimum as regards these factors along with favorable conditions of atmospheric humidity and soil nutrients. Hence, little can be accomplished by control of the environment.

The second method of attack is indirect and less obvious in its details. The resistance of a plant to an infection is essentially a function of its physiological tonus. And that tonus is conditioned by (1) the environment and (2) the genetic composition of the plant. The environment, as we have already said, must for the most part remain uncontrolled. We are left no choice but to utilize whatever features of genetic constitution we can lay our hands on as the only available material in our attack. In the banana as in most plants, not all varieties are equally susceptible to the Panama disease. The most feasible solution of our problem is therefore to utilize these natural immunities as far as possible.

In most bananas, and in all those which are of importance as commercial foods, the capacity for sexual reproduction has been reduced or completely lost (D'ANGREMOND, 2). In a fruit used for food, the condition of parthenocarpy (see NOLL, 42), resulting in the absence in the fruit of any hard seeds or carpellary tissues is a decided advantage and it is easy to see how these features might have been sorted out and perpetuated by the aboriginal horticulturists of the tropics. This selection has finally resulted in the cultivated bananas of today. Unfortunately the best of those grown in the western hemisphere, the Gros Michel¹, is also the most susceptible to the disease under consideration. In our present state of knowledge, this sterility makes it impossible to utilize the desirable features of the Gros Michel by cross breeding it with immune varie-

¹ "This is the standard commercial banana. — It was introduced into Jamaica about 1836 by JEAN FRANÇOIS POUYAT, a French botanist and chemist who settled in Jamaica in 1820. He possessed a coffee property, 'Belle Air' in Saint Andrew and on his return from a visit to Martinique planted this banana on his estate. At first known as the 'Banana-Pouyat', it gradually became known as the 'Martinique Banana'. — From this one plant have grown the millions of bananas that are now cultivated in Jamaica, while the commercial plantations of Central America and of Cuba are, we believe, of the same origin." (In FAWCETT, 13) We thus have no record of how and when this variety arose. DR. OTTO REINKING believes it to be identical with the "Pisang Ambon" of Malaya (53) but the chromosome studies recorded in Part III of the present paper do not support this hypothesis.

ties, as would be done with any normal seed forming plant. The banana is, it is true, subject to frequent bud mutation, as is evident from the frequent occurrence of sectorial chimeras¹, but the chance of one of these mutants being such a plant as we wish is entirely too remote to satisfy our needs. We are therefore forced either (1) to find some means of overcoming, at least occasionally the sterility of the Gros Michel, thus making it available for breeding experiments or (2) to duplicate the desirable features of the Gros Michel in a banana of other parentage. Our first problem is to find the cause of this sterility.

Before taking up this question it will be necessary to state briefly some general taxonomic features of the genus under consideration. The genus *Musa* is divided into three subgenera: (1) *Physocaulis* BAK., (2) *Eumusa* BAK., and (3) *Rhodochlamys* BAK. (SCHUMANN, 60). The distinctions between the last two are slight and seem quite artificial. Hence in the following treatment they will be considered together under the name *Eumusa*. The first group, however, sets itself off sharply from the Eumusae by its few, large and smooth seeds, the very large number of flowers per bract and its non-stoloniferous habit as well as other minor features of systematic value. It is of little importance commercially since the fruit is inedible, only the base of the young stem being eaten (see BRUCE, 13). The Eumusae were originally restricted to the south-eastern portions of Asia, Malaysia and Oceania but are now cultivated throughout the tropics of the world². The Physocaulidae on the other hand are most abundant in Africa, where they constitute the only indigenous Musas. This subgenus is represented in Asia by two indigenous species in northern and Farther India and one probably introduced species in Java (SCHUMANN, 60). *Musa glauca* ROXB. which is found in Farther India, shows many transitional features between the Physocaulidae and the Eumusae.

Our only geological record is of the Physocaulidae and hence gives us no clue to the origin of sterility in the Eumusae. It is of interest, however, for other reasons. Seeds of *Musa ensetiformis* BERRY, which are

¹ Mr. W. MALINO SMITH, in the Agricultural News (Grenada) Vol. VI says: "I picked a bunch of claret bananas which contained two hands of green colored fingers and one hand of both claret and green fingers. There was one finger which was half green and half claret. The green fingers ripened yellow." The writer has observed the same phenomenon as well as cases in which green suckers arose from red "bits" and vice versa.

² From their evident relationships as well as from the meagre historical records it seems almost certain that all of the Eumusae found today both in Africa and in America were introduced from southern Asia; the former not earlier than the beginning of the Christian era on the east coast, and of the early fifteenth century on the west coast; the later in the early part of the sixteenth century. (See below.)

almost indistinguishable from those of the present day *Musa ensete* J. F. GMEL. of Abyssinia have been found in the Tertiary coal measures of Colombia where the genus is entirely unknown today (BERRY, 8). Leaves of the form genus *Musaphyllum* GOEPPERT have been recovered from the Tertiary and later eras of Java, Central Europe and North and South America but their identity with the genus *Musa* is by no means certain (BERRY, 7, 8). We have no geological record, so far as I have been able to discover, of any of the tuberculate-seeded *Eumusae*.

Likewise, the first written record of any banana that we have today, that of MEGASTHENES (34) in 303.(?) B. C. probably referred to *Musa superba* ROXB. (See PICKERING, 47), one of the Physocaulidae, and not to a *Eumusa*, for he said "σιτέσθαι δὲ τῶν δένδρεων τὸν φλοιόν"¹ in speaking of a plant which agrees with the description of the banana and which (48) bears the same name as that used later by PLINY for this plant (καλέσθαι δὲ τὰ δένδρεα ταῦτα τῇ Ἰνδῶν φωνῇ Τάλα καὶ φρέσθαι ἐπ' αὐτῶν κατὰπερ τῶν φοινίκων ἐπὶ τῇσι κορυφαῖσιν οἷά περ τολύπας")² (MÜLLER, 39). However, it seems almost certain that a *Eumusa* existed in the Punjab at the time of the Alexandrian invasion for THEOPHRASTUS (69) and following him PLINY (48) speak of it³. We have an even clearer record in the frescoes of the cave temples of Ajunta (443 B. C.), GRIFFITHS (26) in west central India, which can unquestionably be referred, not only to the *Eumusae* but to *Musa paradisiaca*. These frescoes represent a fruit in a high state of cultivation and development; and almost certainly parthenocarpic.

In the interim between the tertiary and the fifth century B. C. our direct record is blank. From then on the records become more numerous, but even in the early centuries of the Christian era the banana was known in the west only from specimens cultivated in the gardens at Alexandria and elsewhere, and neither the early Hebrews nor the Egyptians have left any record of it. Among the Arabs of our era, however, MOHAMMED (36), SERAPIAM (61), AVICENNA (3), et. al., (see D'ORTA, 43) knew it well

¹ "That they use as food the inner bark of the trees". "That in the language of the Indi these trees are called 'Tala', and that fruit like clews (of yarn) grows on them as on the tops of date palms."

² THEOPHRASTUS (69) says: „Ἐστὶ δὲ καὶ ἕτερον δένδρον καὶ τῇ μεγέθει μεγά καὶ ἡδύκαρπον Θεωμασιῶς καὶ μεγαλακαρπον.

³ Ἐτερον δὲ οὐφύλλον τὴν μὲν μορφήν πρόμνηες τοῖς τῶν στρούθων περὶοῖς ὁμοιον.

⁴ Ἀλλὰ τέ ἐστὶν οὗ ἡ καρπὸς καὶ οὐκ εὐθύς ἀλλὰ σκολιὸς ἐσθιάμενος δὲ γλυκύς. ("there is also another tree which is very large and has wonderfully sweet and large fruit. — There is also another tree whose leaf is oblong in shape, like the feathers of the ostrich. — There is also another whose fruit is long and not straight but crooked, and it is sweet to the taste'). PLINY (48) is probably right, however, in considering this to apply to three phases or varieties of the one plant which he calls 'PALA', the 'ΤΑΛΑ' of MEGASTHENES.

from the gardens, and our name '*Musa*' has come down to us from the sanscrit '*moṣa*' through them (WATT, 75).

Although we thus have no direct record of bananas before the fifth century B. C., we do have some indirect evidence in the linguistics of southern Asia. The Aryan name of the banana — for fruit in general if we are to believe PLINY — in the time of MEGASTHENES was *Tala* or *PAIA*. This same root has come down to us in the Hindustani "*Quelli*" in the time of D'ORTA (1535) (43) and in the various permutations of today, — "*Kala*", "*Kadla*", "*Kadli*", "*Kali*"¹, "*Kladi*", "*Klui*", etc., all of them extant in various parts of India today, and probably also in the "*Chuoi*" of Farther India, Siam and Cochin China. This name certainly dates from the entrance of Old Sanscrit into India in the second millenium B. C. and may quite conceivably have been taken over from a previously existent Dravidian name (GRANT, 24). Parallel with this there exists a quite distinct series in the Malay tongues, the "*Piçam*" of D'ORTA (43) being certainly the Malay "*Pisang*" of today. The Tagalog "*Sabang*" may possibly be traced to this root. DE CANDOLLE (15) states that a similar series exists in the Chinese tongues but this I have not verified. Since all of these terms apply to the parthenocarpic varieties of *Eumusa*, we can safely assume with DE CANDOLLE, that these varieties were in existence at the time of the origin of these three tongues, certainly as early as the second millenium B. C. and probably much earlier than that.

Some authors have wished to place the origin of the *Eumusae* on the American continent (COOK, 20, VON HUMBOLDT, 28, et. al.) but the complete absence of fossil records, of any figures in Maya, Toltec, Inca, or other pre-historic pictorial representations (MORLEY, 38) or of indigenous names (MARTIUS, 33), the absence of any authentic records dating back before their possible introduction by the Spanish (for GARCILASSO [23] upon whom VON HUMBOLDT [28] and PRESCOTT [50] lay such stress, wrote in 1564, twenty-nine years after OVIEDO [44] specifically told of their introduction into Peru from Santo Domingo where we know them to have been introduced from the Canaries (OVIEDO, 44]), and the close relation of the American species to those of the East Indies make this highly improbable (see UNGER, 74, and REINHARDT, 52).

From all this it is evident that we can not hope to find direct historical information concerning the time and manner of origin of sterility in the banana. We are forced, therefore, to turn to the other method, of seeking evidence contained in the plant itself as we find it today. We are aided in one way by the fact of sterility, for, owing to this very fact, our present day material has come down to us as a vegetative clone, and

¹ The banana is considered sacred to "*Kali*", the Hindu goddess of fecundity but the connection between this fact and the name '*Kali*' is by no means clear.

thus theoretically the same plant as the original of perhaps five thousand years ago. Obviously our first problem is to examine in detail the flowers of the Gros Michel banana (our standard commercial variety) to determine just where in the individual ontogeny the aberrances, which culminate in the abortion of the reproductive portions, set in, what is their nature, what the observable behaviour conditioning them, and if possible, what can be done to control them. In order to obtain a better perspective of the problem it has seemed best to examine the corresponding stages in a "normal" or fertile variety, and for reasons which will appear later, the clone known as "Rodoc Clamp", a variety of *Musa basjoo* SIEB. et ZUCC., was chosen.

PART II.

Floral Morphology of Certain Species of *Musa*.

As a first step toward the solution of the problem outlined in Part I of the present paper, material was obtained for a complete study of the floral development of two representative varieties of bananas. A fairly complete collection was obtained of all parts of male, female and neuter flowers of the Gros Michel banana, (*Musa paradisiaca* L. subsp. *sapientum* (L.) O. KTZE. var. Gros Michel). Some additional material of the Apple banana (*M. paradisiaca*, subsp. *sapientum* var. Apple) the Chinese banana (*Musa Cavendishii* LAMB), and of the Frog Plantain (*Musa Bakeri* HOOK.) was also collected by the writer, like the first, at the Plattfield Plantation of the United Fruit Company in Jamaica in July, 1926 (see p. 673, footnote 2). Of the first of these varieties, specimens were taken from each hand of each of a number of inflorescences (for general description see SCHUMANN, 60), which ranged from fourteen millimeters in length up to mature bunches of about two meters in length, inclusive of the terminal male portion of the inflorescence. The smallest was of the earliest stage at which the inflorescence could be distinguished from the vegetative growing point. The oldest material was from bunches from which the 'fingers' had begun to fall and from which one hundred or more "male" bracts had already been shed¹. As many intermediate stages were collected as the time available permitted. Each collection was made in duplicate, one being fixed in formol-acetic-alcohol of the modified formula of Chamberlain, the other in medium crom-acetic. The

¹ In most varieties of banana the distal portion of the floral axis, which bears staminate flowers only, continues to develop as long as the plant remains alive and in some cases reaches a great length. This is particularly noticeable in the Physocaulids in which 500 to 600 hands of staminate flowers may open aggregating more than 10 000 flowers. In some varieties, however, as in *M. sapientum* subsp. *seminifera* (LOUR.) BAK. only a half dozen male bracts are formed when the inflorescence is terminated by a compound flower resulting from fasciation and in a few varieties the male portion is completely aborted.

formol-acetic fixative of this formula proved far more satisfactory in many ways and I can strongly recommend it for fixing tissues of *Musa* for general cytological as well as for morphological work. Some additional collections of ovaries from older inflorescences of the Gros Michel were made for me at the United Fruit Company's experimental plantation at Almirante, Panama, by Mr. J. H. PERMAR, and I wish here to extend my hearty thanks to him for his efficient aid.

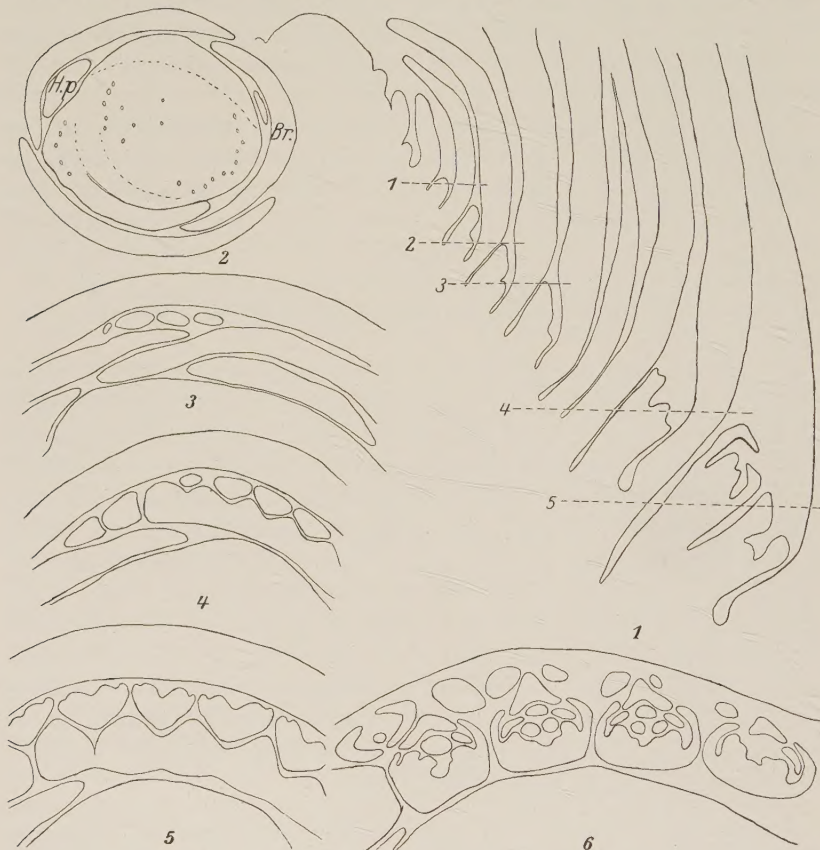
For the study of a fertile seed bearing variety, materials of "Rodoc Clamp" (*Musa basjoo* SIEB. et. ZUCC. [?] var.), a variety originating¹ in the Philippines, were collected and fixed for me by Mr. PERMAR. The writer spent the summer of 1927 at Almirante where the embryo sac development, embryology and seed germination were studied from hand sections and dissections. Additional material was collected at this time and some castration experiments were performed which will be discussed later.

All materials for sectioning were embedded in paraffin in the usual manner. I have employed 4μ sections except where only gross structure was to be studied. This has necessitated in some cases the reconstruction of a single nucleus from several serial sections, but it has also permitted much greater precision in matters of detail than would have been possible with thicker sections. For staining, HEIDENHAIN's Iron Alum Haematoxylin without counterstain has been used throughout. Most of the figures were outlined with camera lucida at the level of the table, using a 1.5 mm ZEISS apochromat immersion objective and no. 18 ZEISS compensating ocular. This gives a magnification of about 3300 diameters. The drawings were finished in detail with a no. 6 ZEISS compensating ocular. Lower magnifications were obtained by modification of the lens system. The photographs were taken with a LEITZ "Makam" camera using Eastman D. C. Ortho plates.

¹ For the sake of uniformity I have used throughout the present treatment, the names under which these clones (for most of them are not true varieties in the sense of breeding true, but only vegetatively propagated descendants of single plants) were sent to the Panama plantations. These names are often misleading and that of this clone is an excellent example of the difficulties which arise. Dr. POPEOE (49) has suggested that this name was probably a corruption of the sub-generic name 'Rhodochlamys', which seemed the more probable from the fact that our records show it spelled in several different ways. The plant itself does not agree with SCHUMANN's (60) description of the Rhodochlamydae but is most closely allied taxonomically to *Musa basjoo*. The same difficulty arises as to "origin" since most of these clones were obtained from gardens and plantations with no certainty that they are actually indigenous in the regions from which they were obtained. It is sincerely to be hoped that the entire collection at Almirante can be gone over carefully in the near future with these points in view, a need emphasized by the observations set forth in Parts III and IV of this paper.

The inflorescence.

The inflorescence of the banana [see detailed description in SCHUMANN (60), PETERSEN (45) and FAWCETT (22)], is a terminal spike rather



Figs. 1-6.

Symbols used: *A. l.* abscission layer, *An.* antipodal, *Br.* floral bract, *C.* carpel, *C. m.* midline of carpel, *E. C.* egg cell, *Ep.* glandular epithelium, *Es.* endosperm, *F.* line of fusion of carpels, *G. c.* generative cell, *H. p.* primordium of hand, *I. i.* inner integument, *M. c.* micropylar collar, *M. p.* micropylar pad, *M. pl.* micropylar plug, *M. t.* mucilage tissue, *N.* nucellus, *N. m.* nucellar mass, *N. o.* nectarial openings, *O. i.* outer integument, *P.* placenta, *Pe.* perisperm, *P. h.* placental hairs, *P. M. C.* pollen mother cell, *P. n.* polar nucleus, *P. T.* pollen tube, *St.* stamen, *Sy.* synergid, *T.* tepalum, *Ta.* Tapetum, *T. l.* tepalum librum, *V. n.* vegetative nucleus.

Figures 1-33 are of the variety Gros Michel. — Fig. 1. Part of longitudinal section of tip of young inflorescence with about 30 axial flower clusters or „hands“ already initiated (200 hands may finally be formed. See note 9), showing growing point of axis, at right sections of primordia of 8 hands with their subtending bracts and at base approximately diametric sections of an adaxial and an abaxial flower of one hand. $\times 62.5$. — Fig. 2. Transverse section at level 1 (of figure 1). Primordia (*H. p.*) of 2 hands just appearing as protuberances axial to the bracts (*br.*) (see text). $\times 62.5$. — Fig. 3. Transverse section at level 2. Upper margin of hand primordium beginning to differentiate into separate flowers. $\times 62.5$. — Fig. 4. Transverse section at level 3. Flower primordia separate but floral parts as yet undifferentiated (see figure 12). $\times 62.5$. — Fig. 5. Transverse section at level 4. Depressions formed in the tip of each abaxial flower primordium indicate beginning of differentiation of floral parts. $\times 62.5$. — Fig. 6. Transverse section at level 5. Floral parts, with the exception of the carpels now well differentiated. $\times 62.5$.

than a raceme since the groups of flowers are sessile and the individual flowers are not subtended by separate bracts (see SCHUMANN, 60, p. 5). The basal portion of the axis is occupied by from one to twenty or thirty hands of pistillate flowers the number varying not only with the variety but also with the cultural conditions¹. Above these is a smaller number of neuter or pseudo-hermaphrodite hands. The remainder of the inflorescence which continues to develop until the plant dies (see footnote 1, p. 678) is made up of staminate flowers only.

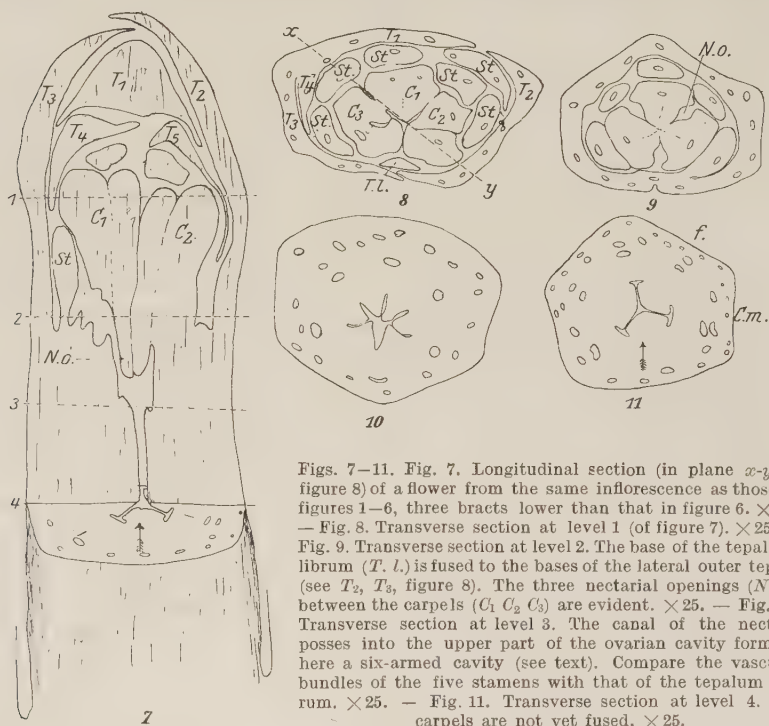
This inflorescence is developed from a single dome-like apical meristem. It becomes differentiated from the vegetative growing point long before the stem begins to elongate, sometimes while the bud is still actually sunk in the broad, slightly concave upper surface of the "bit", like the umbo at the center of the pileus in certain concave-pileated Agarics. The earliest stages which I have examined are taken, therefore, from the very base of the pseudostem (see SCHUMANN, 60), a few inches at most above the level of the ground. The vegetative growing point is a very broad, flat dome as is illustrated in figs. 1 and 12. Each leaf is initiated as an annular ridge which extends about one-third of the way around the circumference of this dome (figs. 2 and 13). This ridge is at first smooth, but before reaching a height exceeding its width its upper margin becomes strikingly corrugated or waved in outline through the appearance of transverse partial folds (radial to the stem) each one of which later becomes vascularized to form one of the veins of the mature leaf. There leaf primordia are very closely packed together. With the beginning of elongation of the stem, however, the originally flat, dome-shaped growing point becomes more conical, the leaf primordia are separated somewhat, and room is left for the intercallation of a second series of shorter annular ridges between them (fig. 1). These secondary axial ridges are the primordia of the small radially compressed flower clusters or hands. Though shorter tangentially, they are thicker radially than are the leaf primordia and are much less distinctly corrugated (fig. 2). The flowers arise from them as a double (in some varieties single) row of closely grouped protuberances which in the Eumusae are usually from fifteen to twenty in number.

Early Development of the Flower.

The individual flower primordia are at first broadly dome-shaped as is the terminal growing point of the stem itself (figs. 3 and 14). As they

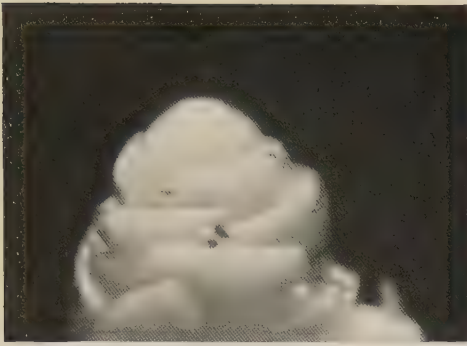
¹ *M. rosacea* JACQ. regularly has only three or four female hands while a good stem of *M. paradisiaca* L. subsp. *sapientum* will sometime have more than twenty hands. I have seen, however, specimens of the Red banana (*M. paradisiaca* subsp. *sapientum* var. *rubra* [?]), growing in abandoned and overgrown plots bearing as few as two good hands, although under better conditions this variety is a very prolific bearer.

grow, however, they become closely crowded together so that each is roughly either square or pentagonal in cross section and almost flat on top. When the individual primordium has reached a height about half its diameter a depression begins to appear on the tip, distinctly abaxial in position (figs. 5 and 15). The marginal ring thus left develops actively at the abaxial radius and 120° from this on either side so that the three outer perianth segments (tepala) are early distinguishable. The tissues opposite the two lateral segments and between them thicken rapidly,

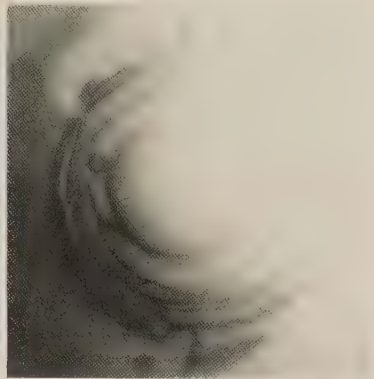


Figs. 7-11. Fig. 7. Longitudinal section (in plane $x-y$ of figure 8) of a flower from the same inflorescence as those in figures 1-6, three bracts lower than that in figure 6. $\times 25$. — Fig. 8. Transverse section at level 1 (of figure 7). $\times 25$. — Fig. 9. Transverse section at level 2. The base of the tepalum librum ($T.L.$) is fused to the bases of the lateral outer tepala (see T_2, T_3 , figure 8). The three nectarial openings ($N.o.$) between the carpels (C_1, C_2, C_3) are evident. $\times 25$. — Fig. 10. Transverse section at level 3. The canal of the nectary passes into the upper part of the ovarian cavity forming here a six-armed cavity (see text). Compare the vascular bundles of the five stamens with that of the tepalum librum. $\times 25$. — Fig. 11. Transverse section at level 4. The carpels are not yet fused. $\times 25$.

forming two of the outer stamens and between them the tepalum librum. This latter remains fused to the outer tepala until much later (fig. 6). The third stamen of the outer ring is formed opposite the abaxial tepalum (figs. 6 and 16). The two lateral tepala of the inner ring are initiated as folds inside the notch between the alternate outer ones, while the two inner stamens arise opposite these. The five stamens and the tepalum librum (see SCHUMANN, 60), in the stage represented in figs. 8-9 and 17-18, form a single ring and the tepalum librum is distinguishable from the rest only by its more diffusely distributed vascular tissue. There is no trace of the missing stamen of the inner ring at any time in the development of the flower and there is no indication in the vascular system



12



13



14



15



16



17



18

Figs. 12-18. Fig. 12. Growing point of inflorescence, lateral view. $\times 30$. — Fig. 13. The same from above. $\times 30$. — Fig. 14. Young hand primordium on which the fingers are just outlined. Compare figure 3. $\times 30$. — Fig. 15. Two hands. In the lower hand the outer perianth segments are outlined. Compare figure 4 $\times 30$. — Fig. 16. Later. The inner members are beginning to be distinguishable. Compare figure 5. $\times 30$. — Fig. 17. All floral parts with the exception of the carpels well formed. Compare figure 6. $\times 30$.

— Fig. 18. The three carpels are just beginning to push out leaving a triangular cavity between. The tepala closing over the inner members. $\times 30$. — (All photographs, with the exception of fig. 130a are reproduced without retouching of any sort.)

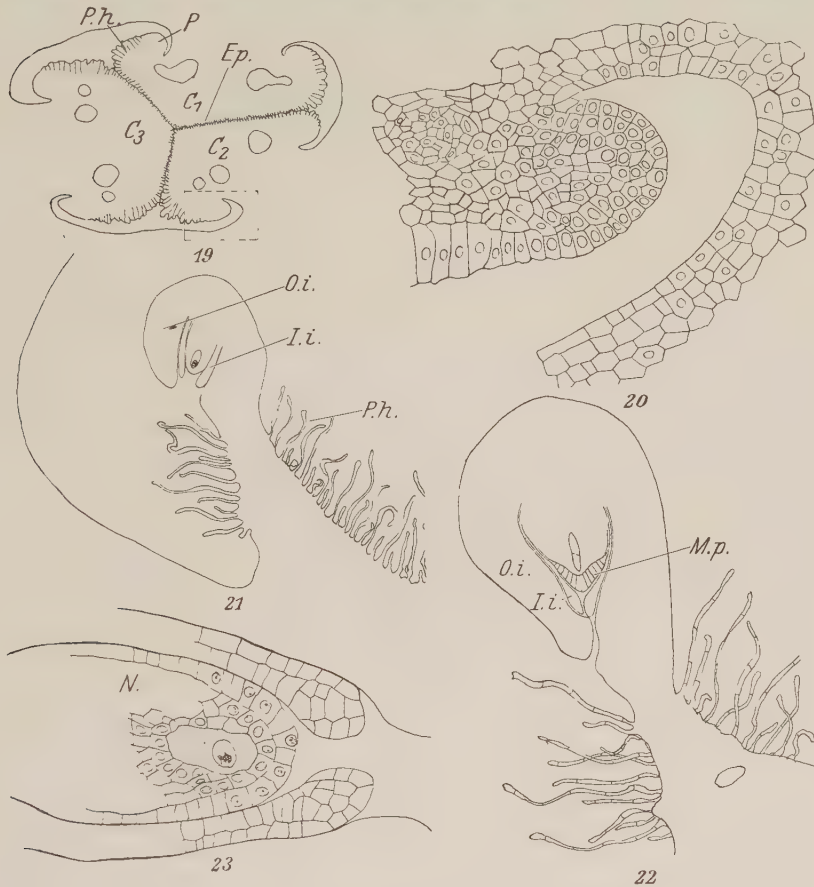
that it has been fused with any other organ. The three carpels are the last floral organs to appear (fig. 18). They arise as protruberence from the bases of the outer ring of stamens and develop rapidly, fusing above so that in the stage represented in figs. 7—11 there is a single columnar style. This has six stigmatic lobes at its apex. The fusion is incomplete at the base so that three radially widened canals are left which communicate between the ovarian cavity and the exterior (figs. 7 and 9, *N.o.*). These openings or sutures are the openings of the nectaries of the mature flower (see WITTMACK, 76). The description given above applies to the early development of all types of flowers and the figures represent the series of stages found in an inflorescence which has been pushed up to considerably less than breast height in the pseudostem and has a total length of ca. 33 mm. It is only later that the flowers become differentiated into female, neuter and male through development of the different organs.

The Female Flowers.

By the time the inflorescence has reached breast height within the pseudostem and has a total length of ca. 120 mm the staminate and pistillate flowers are distinguishable, although at this time the neuter flowers do not differ externally from the female. The ovarian cavity is originally triangular in cross section at the base (fig. 11), through the partial fusion of the three carpels and becomes almost closed and six-rayed above (fig. 10). This upper six-rayed portion does not undergo any essential change during the later development and differentiation of sex of the flower. It is lined with a glandular epithelium which is continuous wherever a more or less protected cavity occurs in the ovary or stigma (fig. 19) and only disappears where the fusion of stigmas or placentae is complete. This is the nectary and it is present in the flowers of both sexes. In the development of the female flowers it is the portion below this which elongates to form the ovary proper.

The ovary, as has been said, is made up of three carpels which are flattened at their bases so as to leave a triangular cavity between (fig. 11) and are fused at their margins. These margins turn in until all six meet at the center (fig. 19). Here they fuse leaving in place of the original three-winged cavity, three separate crescentic ones, the locules. The glandular epithelium is long recognizable in the fused placenta as a double row of columnar cells (fig. 19). Long before fusion is complete these carpellary margins turn back (fig. 19); the rounded ridges thus formed, finally giving rise to the placentae proper. The two placental ridges in each locule thus arise from the margins of the same carpel. When these ridges have reached a radial height of about double their breadth, their growth into the cavity ceases, except where, at regular intervals, the ovules (fig. 21) push out from the placentae.

Meanwhile the glandular cells of the epithelium, particularly on the placental ridge itself, have separated somewhat from each other, laterally, at the same time elongating anticlinally and dividing transversely and thus forming a loose mass of multicellular glandular hairs, "das sogenannte



Figs. 19—23. Fig. 19. Transverse section of ovary. Carpels (*C.*) fused but glandular epithelium (*Ep.*) still evident. Hairs (*P. h.*) on the bases of the placentae (*P.*) beginning to elongate. $\times 50$. — Fig. 20. Detail of one placenta from figure 16. $\times 250$. — Fig. 21. Young ovule with definitive megaspore mother cell. Integuments still open. Note the glandular hairs (*P. h.*) on the placenta. $\times 50$. — Fig. 22. Later stage. Note the micropylar pad, (*M. p.*) at the tip of the nucellus. $\times 50$. — Fig. 23. Detail from the same stage as figure 19. The tapetum is already indistinguishable from the cells of the nucellar tissue while the cells of the micropylar pad (see text) are just beginning to elongate. $\times 250$.

Haarkissen, in dem die Ovula eingebettet liegen" (WITTMACK, 76), (figs. 21 and 22). These are especially abundant around the bases of the ovule primordia where they form a structure seemingly homologous with the arillus of the related dry-fruited Scitamineae (see HUMPHREY, 29). It was the swelling of the gelatinous secretion of these hairs in water which

caused D'ANGREMOND (2) to abandon the use of aqueous fixatives and stains. I have had no difficulty with them after fixing in formol acetic alcohol.

The ovule primordium is at first a slender, finger-like process not more than five cells in width and three or four times that long. All of this development goes on long before the inflorescence has pushed out from the pseudo-stem. Material is therefore difficult to get and my supply has been inadequate for a study of all of its stages. D'ANGREMOND (1, 2) states that the primary archesporium arises from a sub-epidermal cell at a time when the ovule has just begun to bend laterally and when both inner and outer integuments are just initiated (p. 84—85, textfig. 8, 9, 10, Taf. V, 7, 10). The primary tapetal cell is cut off from the outer end of this archesporial cell leaving the inner end as the usually single megaspore mother cell. The tapetum is already indistinguishable from the neighboring nucellar tissues at a time when the integuments are still open and when the nucellus contains only a few hundred cells (fig. 24). The inner integument remains but two cells in thickness throughout the entire development of the seed, while the outer integument becomes thickened to form the major seed coat. Both of the integuments remain open leaving a pronounced microphyllar canal which is recognizable even in the mature seed (HUMPHREY, 29, p. 28, fig. 50 a). At the time that the megaspore mother cell is just entering upon synapsis, that is when the inflorescence is just beginning to show above the pseudo-stem (total length of the inflorescence being then ca. 300 mm.), the cells of the nucellar epidermis under the micropyle begin to elongate perpendicular to the surface of the nucellus, forming the peculiar columnar-celled „micro-pylar pad” (fig. 22), (see HUMPHREY, 29, p. 28). The nucellus, which is at first much longer than broad, now expands laterally, largely through enlargement of the individual cells, so that the ovule becomes nearly spherical (fig. 22). In the Gros Michel banana the ovule has attained almost its maximum size when the megaspore mother cell begins to divide.

Embryo sac development.

The Gros Michel. A sterile parthenocarpic variety of Musa. The megaspore mother cell is about twice as long as broad with very dense homogeneous cytoplasm quite different from that of the surrounding nucellar cells (figs. 23 and 24). Unlike the latter, this megaspore mother cell contains numerous darkly staining rods comparable to the chondriomites of BONNET (11). The nucleus is large, and spherical rather than oval. Although the chromatic granules (prochromosomes?) are clearly evident they have lost their regularity, of both size and form, as compared to those of the prophase in somatic nuclei. The nucleolus is extraordinarily large and stains deeply. The pre-synaptic spireme (fig. 25 a and b),

has every appearance of being continuous but, unlike that described in *Carex aquatilis* (STOUT, 64), the thread is not of uniform diameter, but possesses distinct knots and in parts appears to be double.

The complexity of the post-synaptic spireme is such that it is impossible to trace out and count the individual leptotene loops, but it seems evident that such exist. It is difficult to see these clearly and to draw them so as to show the true relationships of the various parts, but the folds of the thread do not appear to anastomose (figs. 25 a and b). During the leptotene stage the nucleolus becomes lobed, and oval fragments may be seen attached to the spireme here and there. They are sharply distin-



Figs. 24—25. Fig. 24. Detail of megaspore mother cell slightly earlier than in figure 21. $\times 675$. — Fig. 25a, b. Two consecutive sections of nucleus of a megaspore mother cell before synapsis. Note especially the fragments of nucleolar material. $\times 1400$.

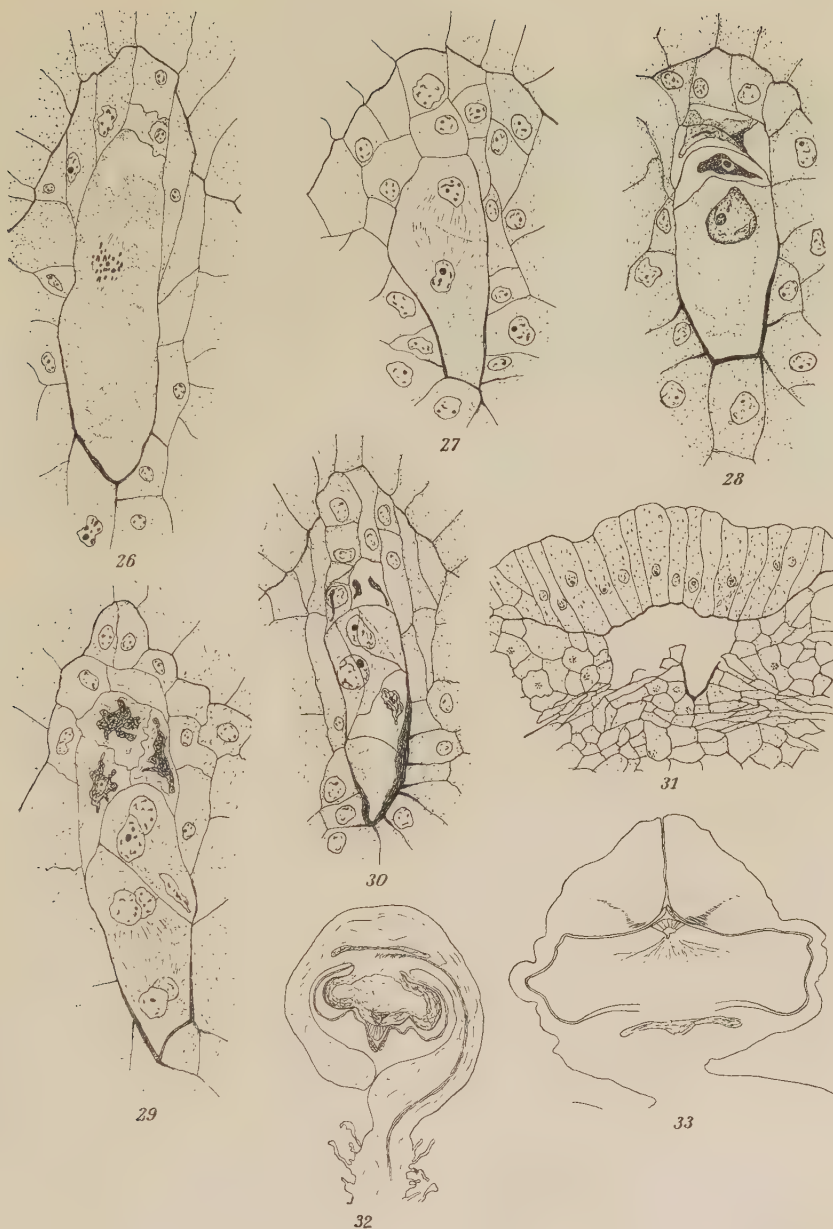
guishable from the spireme knots by their smoother outlines and somewhat paler color, and have every appearance of being thin-walled vesicles (figs. 25 a and b).

I have not attempted to study all of these stages in as minute detail as a purely cytological study would require. The stages, between this and the first meiotic spindle, have not been observed in the embryo sac mother cell, but may be assumed to resemble those found in the corresponding phases in the pollen mother cell described below. The nucleus has lain throughout this time in the upper third of the megaspore mother cell. The first meiotic spindle is formed parallel to or slightly oblique to the long axis of the cell (fig. 26). The chromosomes at this time are very small and only slightly longer than broad. They are often scattered over a considerable portion of the spindle. My material of this stage is inade-

quate for conclusively definite counts, but since my figure 26 shows thirty chromosomes, we may assume that D'ANGREMOND's (2) count of thirty-two at this stage was correct. (See also Part III for somatic counts.) Certain of these chromosomes show distinct indications of the incipient homeotipic split, but since I have been unable to observe the entire complement, the relative numbers of bivalents and univalents could not be determined here. The two daughter nuclei are organized regularly and a separating wall laid down on the spindle (fig. 27). The upper cell of this pair may or may not divide again. In the latter case it begins to degenerate immediately. Where division does take place the spindle usually lies parallel to the first one, but may lie in any plane whatever (see TISCHLER, 71, and D'ANGREMOND, 2). The meiosis II spindle in the lower cell is also parallel to that in meiosis I and the upper cell of the resulting pair also degenerates, and although two, and sometimes three, crushed and degenerating megaspores are at times still to be observed after the large megaspore or definitive embryo sac mother cell nucleus has been developed (fig. 28), they soon disappear completely.

The first spindle in the embryo sac proper is usually oblique to the axis of the cell. Karyokinesis and the partial reorganization of the daughter nuclei proceeds normally. This spindle, however, instead of breaking down immediately as is usual in embryo sacs, proceeds to lay down a wall and the sac is thus separated into two distinct cells. The nuclei rapidly undergo a second and third division so that an eight-nucleate female prothallus is formed, but since a cross wall has followed each nuclear division, these eight nuclei are enclosed in separate cells. The two polar nuclei which would ordinarily fuse to form the primary endosperm nucleus, are separated by a definite wall, and the usual organization of the embryo-sac is made practically impossible (fig. 29). Such a condition is not unknown elsewhere, for it has been reported by ROSENBERG (55) in his *Drosera* hybrids, but it is sufficiently unusual to be worthy of special note.

Although it seems probable from the occasional occurrence of seeds in the Gros Michel, that the embryo sac may sometimes develop further on normal lines and may even at times form a functional egg, such cases must certainly be very rare. What I have described above is the most advanced organization of an embryo-sac that I have observed in this variety (see also TISCHLER, 71, and D'ANGREMOND, 2). Usually degeneration sets in immediately after diakinesis, that is with the formation of the first meiotic spindle. Often supernumerary nuclei ("sonderkerne") are formed as a result of the tendency of certain chromosomes to lag, in which case degeneration of the whole cell sets in, without further spindle formation. Often both on this and on the subsequent spindle, wall formation seems to be more or less divorced from spindle formation so that



Figs. 26—33. Fig. 26. Meiosis I. The chromosomes are scattered. Note the thickened basal wall of the megaspore mother cell. $\times 750$. — Fig. 27. Interkinesis after Meiosis I. $\times 750$. — Fig. 28. Definitive megaspore with three degenerating megaspores above. The definitive megaspore nucleus is very large and irregular. $\times 750$. Fig. 29. An embryo sac with seven nuclei visible with definite wall across the middle and indications of formation of other walls. (See text.) The three degenerating megaspores are still distinguishable. $\times 750$. — Fig. 30. A very irregularly organized embryo-sac with numerous dividing walls. Such a prothallus soon goes to pieces. $\times 750$. — Fig. 31. A disorganized embryo-sac. Note the nucellar tissue breaking down at both sides. $\times 250$. — Fig. 32. Sagittal section (through funiculus) of ovule with collapsed nucellus and inner integument while externally the seed is plump. $\times 25$. — Fig. 33. "Horizontal" section (perpendicular to that in figure 32) of an entire seed which has collapsed. $\times 25$.

"protoplasts" are often cut off which contain no trace of nuclear material. Such a condition closely resembles that described by BUSCALIONI (14) in the intercotyledonary endosperm of *Vicia*, *Pisum*, etc., and seem indicative of a disturbed general metabolism of the regions concerned. Even where a definitive embryo sac mother cell is formed the nucleus is often irregular of pyriform (fig. 28) as if through incomplete fusion of the "Karyomerites" (see CHODAT, 18). With the degeneration of the embryo sac or embryo sac mother cell the nucellus breaks down around it (fig. 31), the seed collapses, and thus is formed the fungiform cavity which HUMPHREY (29) thought represented the embryo sac. Sometimes the seed collapses as a whole, giving it the flattened form illustrated in fig. 33. Often, however, only the nucellus and inner integument collapse, leaving the seed round and plump externally as if quite normal. Such seeds may attain a diameter of two or three millimeters, before showing any external signs of degeneration (fig. 32). This entire process is completed by the time the first bract opens so that by the time pollen of any sort can possibly reach the stigma, the egg nuclei are already gone.

Although such abnormalities in behaviour are characteristic of many hybrids (ROSENBERG, 55, 56; TISCHLER, 73, et. al.) they are so common in cases of disturbed metabolism in general (NĚMEC, 41; JARETZKI, 30, et. al.), that no conclusions as to the possible hybrid origin of the banana can be drawn from these alone (see D'ANGREMOND, 2).

Since the development of the ovary proper is not apparently related to the question with which we are here concerned, I shall simply refer to the treatments of this phase of development by D'ANGREMOND (2), GREVE (25), TEODORO (68), et. al. The stamens of the female flowers are left sterile through complete failure of the anther sacs to develop. The filament is usually quite normal in length and thickness and is surmounted by a short connective on which the pollen sacs (microsporangia) are replaced by a mass of glandular hairs very similar to those on the placenta (fig. 56). The hairs from adjacent stamens often intertwine so as to form a continuous sticky ring. Only occasionally is there any sign of abortive archesporial tissue in the anther and even the connective is very slender and weak.

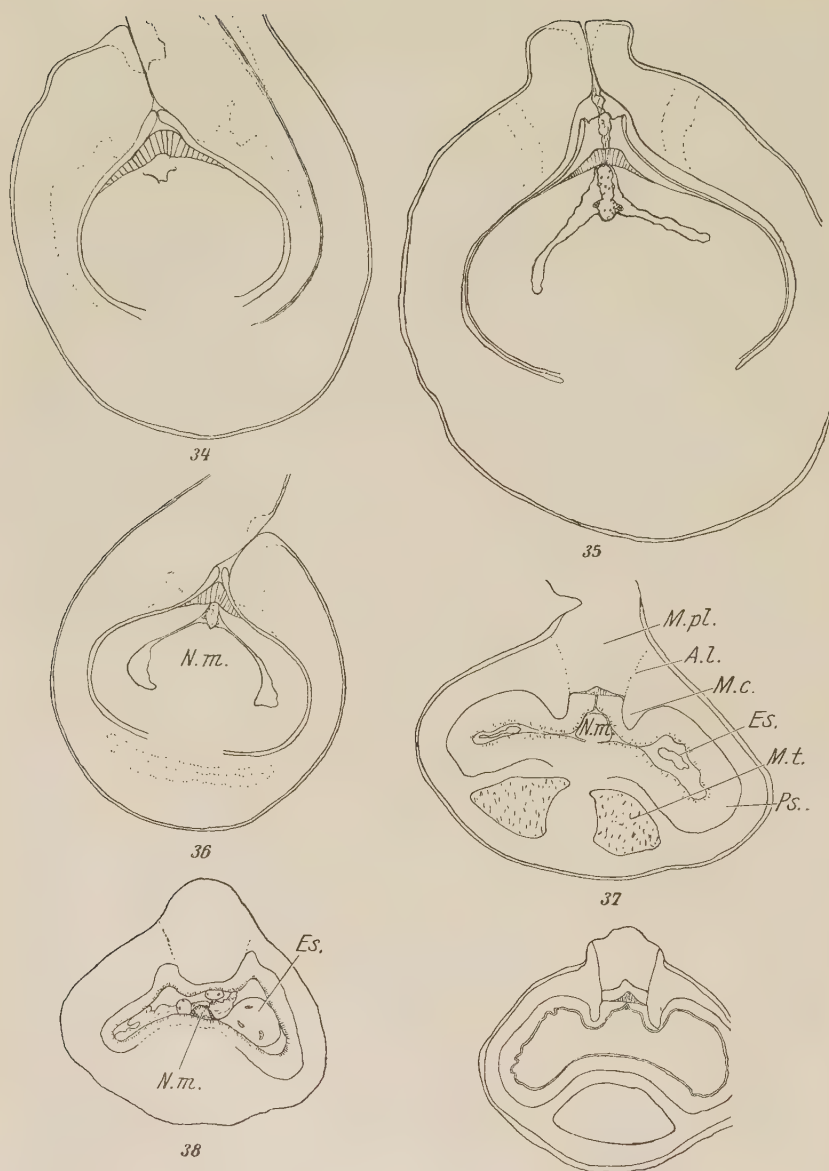
Embryo sac development in a normal, seeded variety. Rodoc Clamp.

My observations have led me to believe that embryo sac development goes on in quite the same way in both fertile and sterile varieties of bananas up to the completion of the definitive archesporium, and that the final organization of the ripe embryo sac in the fertile varieties is simply a consummation of the process already described as starting in the sterile varieties. I have therefore not studied in detail these earlier stages of the fertile varieties. Materials of this variety were collected for me by

Mr. PERMAR, beginning with the first appearance of the inflorescence above the crown. These therefore show the embryo-sac already completed and ready for fertilization. The egg cell is found at the micropylar end accompanied by the two synergids, which later often degenerate. The polar nuclei migrate toward the base of the embryo sac and do not fuse until after the sperm nuclei have entered the embryo-sac. These polar nuclei are occasionally accompanied by one or more antipodals (fig. 40—43) but more often they too degenerate, leaving an embryo-sac containing an egg, one or two synergids and two unfused polar nuclei. This is evidently the condition illustrated by D'ANGREMOND (2), Taf. VII, 6, in which his 'antipoden' are, as I believe, the polar nuclei.

Meantime the tissues of the nucellus lying subjacent to the integument and extending from the walls of the embryo-sac outward and downward to the chalaza begin to break down to form an inverted funnel-shaped cavity with the main mass of the nucellus in the center (figs. 35—39). This autolytic process is quite independent of the development of the embryo-sac itself, (see TISCHLER, 71) and gradually extends downward and then inward until the central mass of nucellar tissue is completely cut off at the chalazal end and is left suspended in the cavity by the embryo-sac alone. In most cases, as was shown by hundreds of dissections, this mass is not completely digested until some six weeks after fertilization when a definite cellular endosperm begins to form (see below).

The banana is insect pollinated and pollination takes place as soon as the bracts begin to open. I have not attempted to follow the pollen tubes down the pistil, but they have reached the gelatinous mass surrounding the ovules within forty-eight hours of the time the bract first opens. It seems probable that they follow the glandular canal which penetrates the stigma (see above), much as they do in *Sarracenia* (SHREVE 63). The tube enters the open micropyle and pushes into the micropylar pad directly over the embryo-sac. I have not actually observed the fusion of the polar nuclei nor of a sperm nucleus with these or with the egg nucleus, but these fusions may all be assumed to occur from the subsequent behaviour of egg and polar nuclei. The egg, however, remains dormant for about six weeks after pollination. The definitive endosperm nucleus undergoes a rapid series of divisions while the embryo-sac itself begins to push out into the cavity left by the breaking down of the nucellar tissues (figs. 35, 42—43). These divisions are, however, certainly not synchronous. Most of the first dozen or more nuclei formed pass into a resting state and are to be seen as large, somewhat irregular, pale-staining nuclei quite evenly distributed about the wall of the developing embryo-sac. Isolated nuclei, however, which appear smaller, more spherical and more deeply staining, continue to divide rapidly forming isolated clusters of small nuclei. The endosperm walls adjacent to these active clusters of



Figs. 34—39.

39

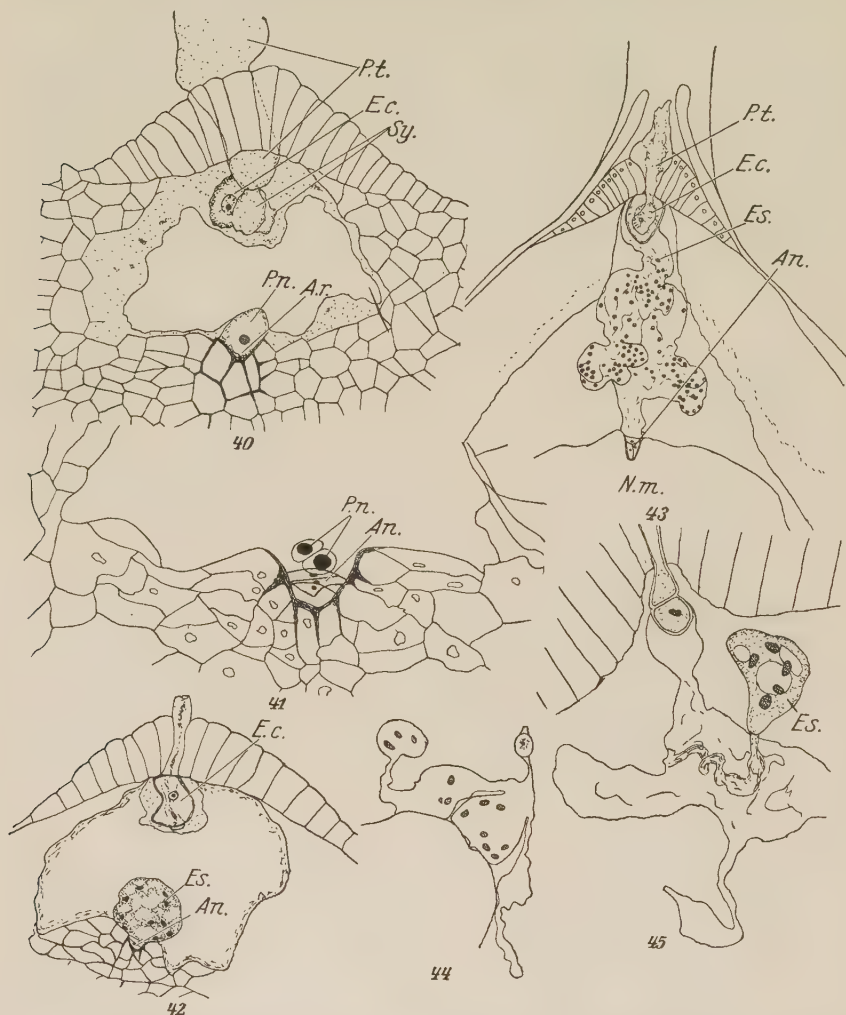
Figures 34—51 are of the variety *Rodoc Clamp*, and with the exceptions of figures 41—43, are from living material. Fig. 34. Sagittal section of ovule at the time of pollination. The embryo sac has pushed out slightly to the sides. $\times 62.5$. — Fig. 35. Horizontal section of ovule 48 hours older. The nucellus has broken down at the sides leaving the embryo sac suspended. The pollen tube has penetrated the micropylar pad and the endosperm nucleus has begun to divide actively. $\times 62.5$. — Fig. 36. The degeneration of the nucellus has extended further around the sides leaving a globular mass of nucellar tissue (*N. m.*) in the center. $\times 50$. — Fig. 37. Horizontal section of

nuclei expand more rapidly than the remaining portions, forming distinct vesicles which extend laterally into the nucellar cavity. Thus sections taken within a hundred hours of pollination commonly show the general outline of the original embryo-sac maintained, with its upper end attached to the base of the micropylar pad (the tapetal cells are very early crushed and destroyed), its lower end still attached to the now free-lying central mass of nucellar tissue, and extending from its sides into the cavity between this nucellar mass and the perisperm, one or more of these endosperm vesicles (figs. 43—45). As the endosperm continues to develop these vesicles may themselves become lobed in a similar manner. The lobes often become completely constricted off from the parent-sac, attach themselves variously to the perisperm wall and develop as separate endosperm masses. These falsely suggest a series of apogamous embryos, and were at first quite puzzling. This behaviour is the rule in the clones designated (see in note 1, p. 679), as Bolo, Philippine Unidentified, Rodoc Clamp, Coolie Hongkseng, etc., and hence is probably characteristic of the fertile *Eumusae* in general. It seems to be associated with the early autolysis of the nucellar tissues, for occasionally the nucellus, instead of degenerating at the sides only, breaks down throughout, though more slowly, and in these cases the more usual single continuous endosperm is formed, which completely fills the ovule (fig. 39).

During this preliminary formation of a simple or compound, non-cellular endosperm, the seed increases rapidly in diameter and the nucellar cavity correspondingly spreads out laterally. It does not, however, become appreciably deeper, for the tissues lying between the chalazal vascular bundles and the outer layer of the seed coat break down into a mucilage tissue (TISCHLER's "degenerations Gewebe", 71) which swells to take up the entire increase in this diameter. The cavity, instead of being subglobose (except for the central nucellar mass) thus becomes flattened and fungiform and this nucellar mass is pushed up against the micropylar region (fig. 37). The integument immediately around the micropyle also thickens rapidly, pushing into the cavity to form the so-called micropylar collar (fig. 37). (See HUMPHREY, 29.) The egg cell, remaining as it does attached to the micropylar pad, thus finds itself at the top of a narrow dome whose sides are formed by this collar (fig. 37). A cylindrical sheet of tissue of the outer integument throughout its thickness and just above the collar, becomes differentiated into an ab-

ovule six days after pollination. The ovule has expanded laterally while the mucilage tissue (*M. t.*) at the chalazal end has swollen to force the nucellar mass (*N. m.*) well up into the micropylar end. The micropylar collar (*M. c.*) is well formed and the abscission layer (*A. l.*) around the micropylar plug (*C. pl.*) is already differentiated. The egg cell has not yet begun to divide in this ovule. $\times 12.5$. — Fig. 38. Section of an ovule 28 days after pollination. Note the numerous endosperm vesicles quite unconnected with the micropylar region. The nucellar mass (*N. m.*) is almost digested. $\times 12.5$. — Fig. 39. Horizontal section of ovule of same stage as that in figure 38. In this case no nucellar mass was present and the embryo sac has filled the entire cavity. $\times 12.5$.

scission layer which cuts out the "micropylar plug" (fig. 37). This plug is thus made up of tissue of the outer integument, including a portion of the vascular bundle and is pierced in the center by the micropyle.



Figs. 40—45. Fig. 40. Longitudinal section of young embryo sac with the egg cell (*E. c.*) and the two synergids, (*Sy.*) The antipodals (*An.*) have degenerated and the polar nuclei have apparently passed to the lower end of the embryo sac and fused (*P. n.*). The pollen tube (*P. t.*) lies beside the egg apparatus but the male nuclei have presumably not been discharged. $\times 250$. — Fig. 41. Base of young embryo sac showing the two polar nuclei (*P. n.*) and three antipodals (*An.*). (Compare D'ANGREMOND 2, fig. 6.) $\times 250$. — Fig. 42. Young embryo sac with pollen tube (*P. t.*) and egg (*E. c.*). The endosperm nucleus has begun to divide forming a tennucleate endosperm (*E. S.*) which is quite separated from the egg. (Reconstructed from a number of successive sections.) (Compare D'ANGREMOND 2, fig. 7.) $\times 125$. — Fig. 43. Longitudinal section (reconstructed) of older embryo sac containing about 100 endosperm nuclei. The sac does not fill the nucellar cavity and its surface is covered with irregular vesicles (see text). Note the absence of nuclei in the basal region. $\times 125$. — Fig. 44. Detail of an endosperm vesicle. $\times 250$. — Fig. 45. A similar stage to fig. 44. $\times 250$.

The egg cell remains dormant throughout this period and first divides when the seed has attained its full size of ca. five millimeters in diameter, that is, three or four weeks after the pollen tube has penetrated the micropylar pad to the embryo-sac. The first division is oblique to the ultimate long axis of the embryo (figs. 47 and 48) and is followed by several other divisions which give rise to a 15—20 celled globular pro-embryo (figs. 49, 50). The suspensor may consist of one or two small cells or it may be entirely indistinguishable (fig. 51). One or both of the synergids may remain intact for a long time and one or both may occasionally undergo one division. The embryo formed from this globule of cells continues to develop into an ellipsoidal mass without differentiation of specific organs. By two months after fertilization it nearly fills the space inside the micropylar collar¹. It does not actually reach the seed cavity proper until much later.

The endosperm remains coenocytic until about ten weeks after pollination. Cell walls are first laid down inside the micropylar cavity around the pro-embryo. Once started this proceeds rapidly until the entire micropylar and nucellar cavity is filled. The cells themselves at first contain isolated starch grains which, however, soon aggregate into the unusually large, angular, compound grains observed by WITTMACK (76, p. 76). Often, however, even in seeds which contain embryos, the endosperm fails to develop, leaving an empty cavity. The embryo continues to grow until it fills the micropylar cavity as a short cylindrical body, and finally pushes out into the main nucellar cavity. Where it encounters the dense, nutritive endosperm, the protruding portion flattens out against this to form the fungiform digestive pad characteristic of the embryos of *Musa* (see WITTMACK, 76; CATIN, 16, 17, et. al.). When, however, the endosperm fails to form, as is the case in most of the "sterile"² seeds developed by so many varieties, this pad, encountering no resistance, emerges from the micropylar collar as an irregular mass, generally

¹ Observed in "Philippine unidentified". My stay at Almirante was not long enough to allow me to follow all these stages through on an inflorescence which I had pollinated myself. Some of these later stages are consequently taken from apparently similar varieties which had been pollinated before my arrival.

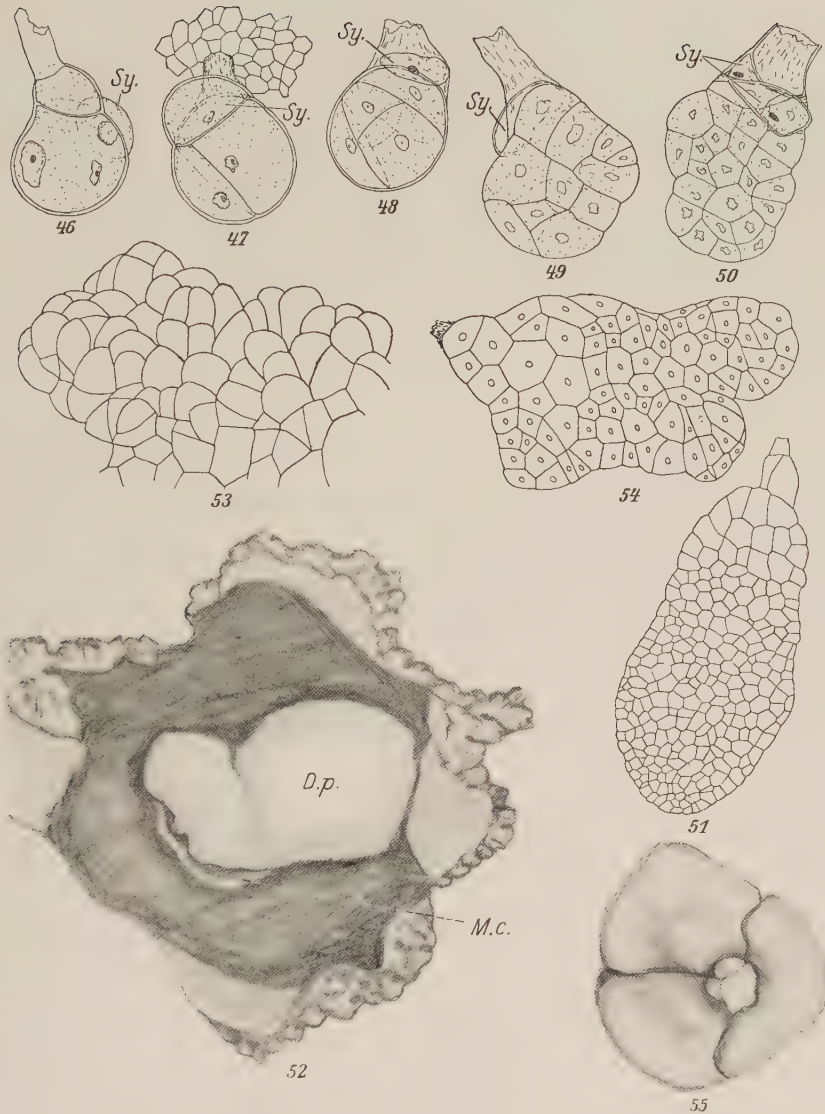
² When dealing with large quantities of seeds we have made a practice of separating the "fertile" from the "sterile" seeds by placing them in a vessel of water, the fertile seeds sinking to the bottom and the sterile ones floating. In control plantings we have never succeeded in germinating one of these „sterile“ seeds while a good percentage of the „fertile“ ones did germinate. An examination of the seeds themselves shows that many of these sterile seeds possess well developed embryos and their sterility is apparently due to the more or less complete absence of nutritive materials. Since this condition occurs very frequently in such theoretically important hybrids as DUNLAP's Seedling × Bastard Hemp (see Parts III and IV) it might prove interesting to attempt to grow these embryos on artificial nutrients (see PFEFFER [46]).

growing to one side, quite suggestive of its cotyledonary origin (fig. 52). The only differentiated portion of this entire embryonic mass in the mature seed is the stem growing point which is formed in a depression at the side of the embryo, well up within the micropolar collar. CATIN (16) has given an excellent treatment of the mature embryo and its germination in several varieties so that I need not go into it here.

M. seminifera (*M. paradisiaca* L. subsp. *seminifera* [LOUR.] BAK.) and hybrids in which it has served as either pollen or seed parent, show a rather striking modification of this development. The first eight or ten divisions in the pro-embryo take place as described above, but they become less and less regular. The cellular pro-embryo then behaves much as did the non-cellular endosperm. Its surface is thrown into irregular folds and protruberences (figs. 53 and 54), each of which develops into a "bud" that separates off and may, in turn, continue "budding" to give rise to several individual pro-embryos. Most of the many embryos so formed are eliminated by competition, but from one to four of them in each ovule may complete their development into functional embryos. The external form of the embryo complex thus formed is the same as that of one individual embryo in other species (fig. 55), but at germination each develops into a separate plant. Polyembryony, which is usually associated with apogamy of some form (STRASBURGER, 65) is thus in *M. seminifera* of quite different origin since it results from the division of one embryo arising from a single fertilized egg and gives rise to several identical F₁ embryos. This behaviour is evidently analogous to the budding of the suspensor in *Erythronium* (HOFMEISTER, 27).

Neuter Flowers.

Above the female hands in the inflorescence there is a series of usually from five to six hands whose micro- and megasporangia fail to mature. These are the neuter or pseudo-hermaphrodite flowers. The upper part of the ovary in these as in both the definitive male and female flowers is provided with a nectary opening to the exterior through three slit-like mouth in the base of the pistil just above the ovary proper. The ovary is here very slightly longer than is that of the male flowers and as in the latter, it has no true locules, the three irregular openings being lined with glandular epithelium without any further differentiation. The style and stigma are formed as in the female flowers but are somewhat more slender. In neuter flowers from well nourished plants the stamens appear quite plump and healthy. Cross sections show, however, an excessive development of the connective and of the thecal walls so that the locules are almost obliterated. In inflorescences from plants grown on poorly watered and uncultivated ground, the "stamens" in the majority of the neuter flowers are reduced to staminodes similar to those of the true

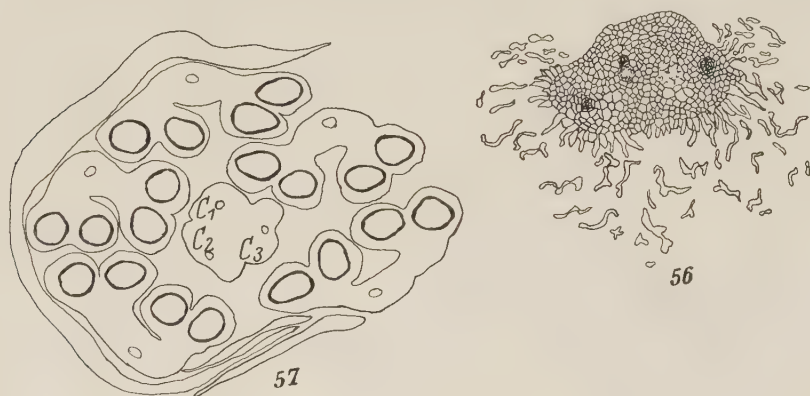


Figs. 46—55. Fig. 46. Detail of egg cell from a living ovule. Note the synergid (*Sy.*) at one side. $\times 750$. — Fig. 47. Fertilized egg after the first division, 4 weeks after pollination. $\times 750$. — Fig. 48. The same showing three divisions. $\times 750$. — Fig. 49. Young pro-embryo of about 20 cells. One synergid (*Sy.*) is still present. $\times 750$. — Fig. 50. Young pro-embryo. Both synergids (*Sy.*) are present, one having divided once. $\times 750$. — Fig. 51. Pro-embryo of several hundred cells. $\times 750$. — Fig. 52. Interior of a "sterile" seed of MARTINI $\times$ DUNLAP'S seedling, seen from the chalazal end. The seed coat has been broken to show the empty cavity, without endosperm, and the irregular digestive pad (cytoledon?) (*D. p.*) of the embryo. $\times 12$. — Fig. 53. Surface of a pro-embryo of *M. semini-fera* showing the tendency of the cells to round off and separate. $\times 750$. — Fig. 54. Pro-embryo (*M. semini-fera*) with three main lobes or "buds". $\times 750$. — Fig. 55. Embryo complex (from a single seed of *M. semini-fera*) made up of three potentially germinable embryos. $\times 12$.

female flowers. In such plants it is evident from the small number of "fertile" hands and also from the fact that individual hands may contain both female and neuter fingers, that adverse environmental conditions have brought about a reduction, some fingers, or even whole hands, which would otherwise have been female being transformed into neuter. (See Note 1, p. 675.)

Male Flowers.

The entire upper distal portion of the inflorescence is made up of male flowers and in most varieties these continue to develop as long as the plant is alive (see note 1, p. 678). In a single inflorescence (Gros Michel) on which the basal fruits were almost mature, I counted ninety-seven scars



Figs. 56—57.

Figures 56—78 are of the variety *Gros Michel*. Fig. 56. Cross section of an anther of a female flower showing the glandular hairs. $\times 50$. — Fig. 57. Cross section of a male flower. $\times 25$.

of fallen male bracts, representing approximately 1500 flowers. The inflorescence would presumably have continued to grow for at least a month longer, and have formed a total of at least 2500 male flowers. As compared with the average of less than 200 female flowers per inflorescence, it is evident what an enormous amount of material and energy is wasted in the production of male flowers, all of which, in such a sterile, parthenocarpic plant, are quite useless.

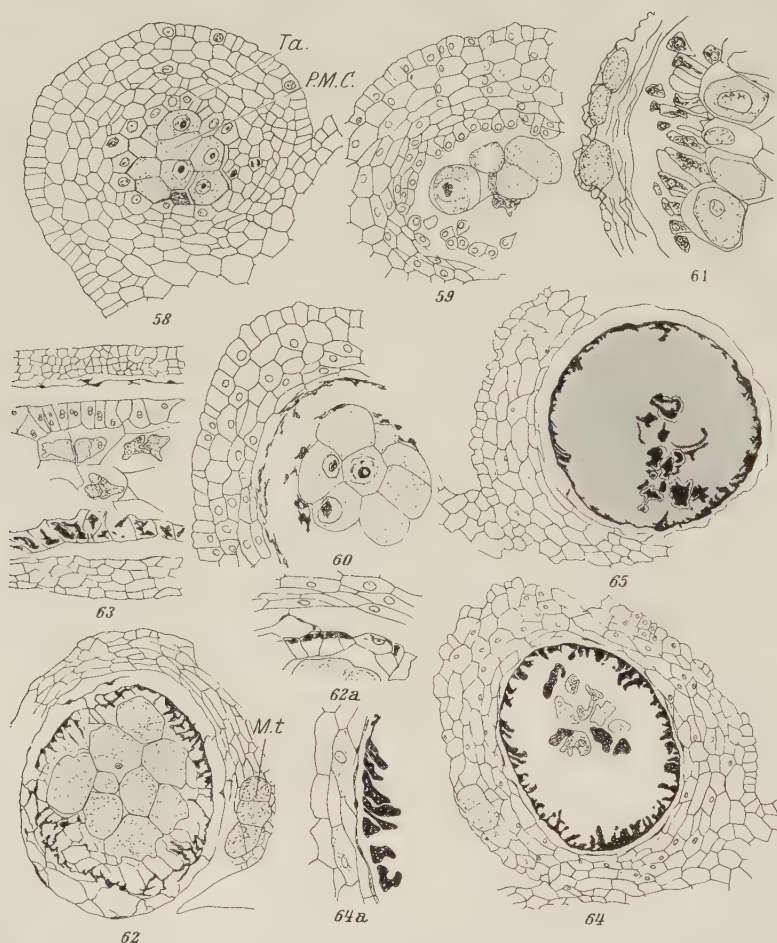
In these male flowers the "ovary" is a trifle shorter than in the neuter flowers and much less plump. The nectary is somewhat more highly developed and the pistil is more slender, and is early blackened throughout, probably by an increased deposit of tannin in the tissues. The stamens do not differ greatly, externally, from those of healthy neuter flowers except in being somewhat longer. The pollen sacs open by longitudinal sutures. It is only in internal structure that they show great differences from those of the neuter flowers.

Development of the Anthers. Gros Michel.

The primary archesporial tissue first becomes distinguishable when the flowers are less than fifteen millimeters in length. The cells at the center of the theca in a single cross section become enlarged, their nuclei increase in size, and the cytoplasm becomes more dense. No mitotic divisions have been observed in the cells of the primary archesporium, the primary and definitive archesporia being thus identical. There is no tangential flattening of cells in the region of the peripheral or transitory layers until later. The tapetum and archesporium form a single continuous tissue, both apparently arising simply by a regional differentiation among the somatic cells (fig. 58). At the time the definitive pollen mother cells begin to round off previous to synapsis the nuclei of the tapetum undergo a single mitotic division without cytokinesis, and when the first meiotic spindle forms in the pollen mother cells, the tapetal cells are uniformly binucleate (fig. 63). I have observed no evidence of either amitotic division or of nuclear fusion in these cells. They may remain intact until the completion of the tetrads or even later. More commonly they soon begin to degenerate, sometimes even before the division of the tapetal nuclei. At the time the pollen mother cells begin to round off the tapetal cells may themselves contract and separate from each other and from the walls of the theca, and are then found lying singly or in groups, some free in the cavity, some clinging to the pollen-mother cells and some still attached to the walls of the theca (fig. 59). In such cases no peripheral layer is formed. Degeneration of these cells may go on until they are to be distinguished only as shrunken, blackened masses. Figs. 58 to 60 represent transverse sections through three locules of a single anther showing (fig. 58) the normal, uninucleate, healthy tapetum (fig. 59), the rounded, free-lying cells and (fig. 60) the blackened protoplasts after degeneration. Such separation of the tapetal cells from the walls of the theca followed by degeneration, or their degeneration *in situ* may set in at any period in the development of the stamen just as in *Rumex* (JARETSKI, 30). More rarely the walls may break down, even quite early in development and the protoplasts escape to form a true periplasmodium. The secretion of slime by the tapetum without rupture of the tapetal walls such as is described by TISCHLER (72) in *Cryptanthus*, may also occur. The studies of COOPER (21) have shown that this slime or matrix (periplasmodium?) is particularly abundant in the sterile varieties and that pollen fertility is on the whole approximately inversely proportionate to its abundance (see Part III).

At the time the pollen mother cell begins to round off its cytoplasm contains many chromidia, as does that in the corresponding stage of the female archesporium. Its nucleus is very large in comparison with the cell as a whole and is quite spherical (fig. 66). The nucleolus is large,

stains deeply, and at this time is extremely even in outline. The peripheral network of the nucleus is very indistinct. Scattered in the nucleoplasm,



Figs. 58—65. Fig. 58. Cross section of one locule of young anther with pollen mother cells) *P. M. C.*), primary tapetal layer (*Ta.*) and wall of anther. $\times 250$. — Fig. 59. The tapetal cells free and rounding off. $\times 250$. — Fig. 60. Cross section of same anther as in figure 58. The tapetum has broken down. $\times 250$. — Fig. 61. A later stage showing the tapetum clinging to the pollen mother cells but separated from the walls of the locule. $\times 250$. — Fig. 62. An older anther with normal tetrads and degenerating tapetum. $\times 250$. — Fig. 63. Longitudinal section through an anther in which the binucleate tapetum is intact on one side and degenerated on the other. $\times 250$. — Fig. 64. An old anther with degenerating pollen grains and broken down tapetum. Neither periplasmodium nor slime has been formed. $\times 250$. — Fig. 65. A locule filled with a slimy matrix. $\times 250$.

however, are numbers of spherical bodies of nearly uniform size staining heavily in iron alum hasmatoxylin. These, by far the most prominent structures in the nucleus, have much the appearance of the pro-chromosomes figured by d'ANGREMOND (2). In no case, however, have I been

able to count more than the haploid number of these bodies and usually the number is less than that. It seems very unlikely that the chromosome pairs could be so completely fused as to give the appearance of single bodies at so early a stage. Hence it seems impossible to consider them as pro-chromosomes. On the other hand, they are certainly not artifacts, for not only can they be clearly seen in living material ("Bolo", *M. acuminata*, etc.), but they stain *intra vitam* with methylene blue¹ much less darkly than does the chromatin network. They are clearly not carbohydrates or fat globules, for they do not stain with either osmic acid or Sudan III, nor do they give a reaction with iodine. They seem, in fact, quite anomalous (figs. 66 and 67).

In fixed materials the nuclear threads are also indistinct at synapsis. The synaptic knot has an appearance quite similar to that figured by LEWITSKI (32) in *Beta*, with a considerable number of oval or spherical globules more or less connected by achromatic strands and imbedded in a refringent, apparently slimy, contracted matrix, which is very difficult to represent in a drawing (fig. 68). In every case where a clear count could be made the number of these globules was exactly the diploid chromosome number, thirty-two. As the material passes to later stages these globules are replaced by threads and the subsequent behaviour leads me to believe that although they do represent the individual chromosomes, they are the result of excessive contraction of the individual spireme loops. It is to be recalled that TISCHLER (70) also reported similar bodies in the synaptic figures in *Musa*. In living material stained in methylene blue these bodies are never to be seen at this stage and are replaced by slender filaments. At synapsis these filaments contract somewhat, but they center around the side of the nucleus nearest the nucleolus and form distinct "bouquets" very similar to those seen by KAUFFMANN (31) in *Tradescantium*. It is impossible, however, to count the number of these loops (figs. 82—84).

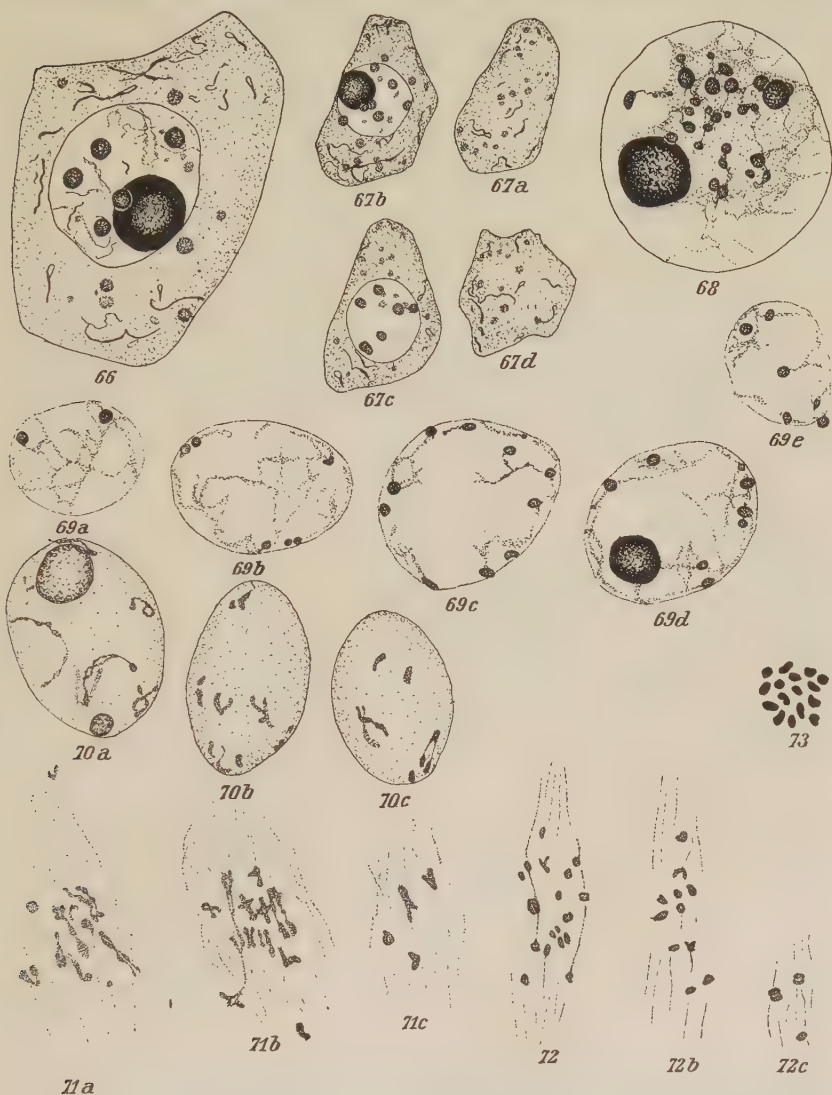
The development of the pollen mother cells, as D'ANGREMOND (2) has pointed out, is continuous from the base of the anther upward, so that late synapses, leptotene, diakinesis and meiotic spindles can be found successively, from the base upward, in a single anther. It is therefore not difficult to determine exactly the sequence of stages which might otherwise be confused. Shortly after the stages considered above, nuclei are to be found in which the chromatic material, with the exception of the nucleolus and occasional stray strands running more or less radially into the nuclear cavity, is again distributed at the periphery (fig. 69). The most prominent features in such nuclei are again the oval, deeply staining chromatic bodies. These are definitely thirty-two in number and many

¹ 1:10 000 solution. This apparently does not kill the cell for some time and excellent preparations could be obtained.

of them show distinct indications of pairing. The figures resemble closely those of ROSENBERG (55) for *Drosera*. To each of these bodies is attached a faintly staining, irregular filament and the whole is somewhat masked by a coarse network of broad, pale bands over the periphery of the nucleus. These bands persist up to the moment of the breaking down of the nuclear membrane and in living material completely hide the chromatic bodies, which only become visible on staining. They are probably thickened regions of the nuclear membrane itself. At this stage, the nucleolus has already begun to shrink and to stain less deeply. The transition from this stage to diakinesis is quite rapid and seems to be largely a matter of dissolution of the broad peripheral bands, leaving the paired chromosomes in the interior unmasked. The chromosome pairs also become more distinct and more closely coupled (fig. 70). Not all of the chromosomes pair, however, but eight of them remain scattered near the nuclear surface, while the other twelve pairs have a tendency to gather more at one side. Such irregularities in the formation of gemini, although mostly known from hybrids (ROSENBERG, 55, 56; BALLY, 5; TÄCKHOLM, 66, et. al.) are not unknown in other plants.

Diakinesis is rather brief and at the moment of the final dissolution of the nuclear membrane the chromatic figure is often pulled out to one side. I have not observed this transition in sectioned materials, but in smear mounts fixed in weak FLEMMING's fluid within five seconds of the time the flower was opened, it is quite noticeable (fig. 85). It is very brief. The completed spindle is usually oriented parallel to the long axis of the anther, and is very long and narrow (see TISCHLER, 70). It is only rarely possible to count the chromosomes in polar view, but such counts as I have been able to make show that reduction takes place at this stage, for sixteen chromosomes are regularly present in such preparations (fig. 73). But in the anaphase the chromosomes often become scattered over the entire extent of the spindle and are then easily counted. On these spindles there are constantly thirty-two chromosomes (figs. 71 and 72). Twelve of these early pass to each pole and show no sign of splitting. These are probably members of the twelve gemini observed at diakinesis and can be considered as normal diads or bivalents. The remaining eight unpaired chromosomes tend to lag near the equator of the spindle somewhat more than do the others, and show a distinct longitudinal split. They are evidently univalents which, being unpaired, have already initiated the homeotypic division (fig. 72). These figures distinctly resemble those shown by BALLY (5) for *Triticum*—*Aegilops* hybrids, by ROSENBERG (55, 56) in interspecific crosses in *Drosera* and *Hieracium*, etc. They are of particular interest here because they represent the first evidence we have encountered which definitely points to a hybrid origin for the banana.

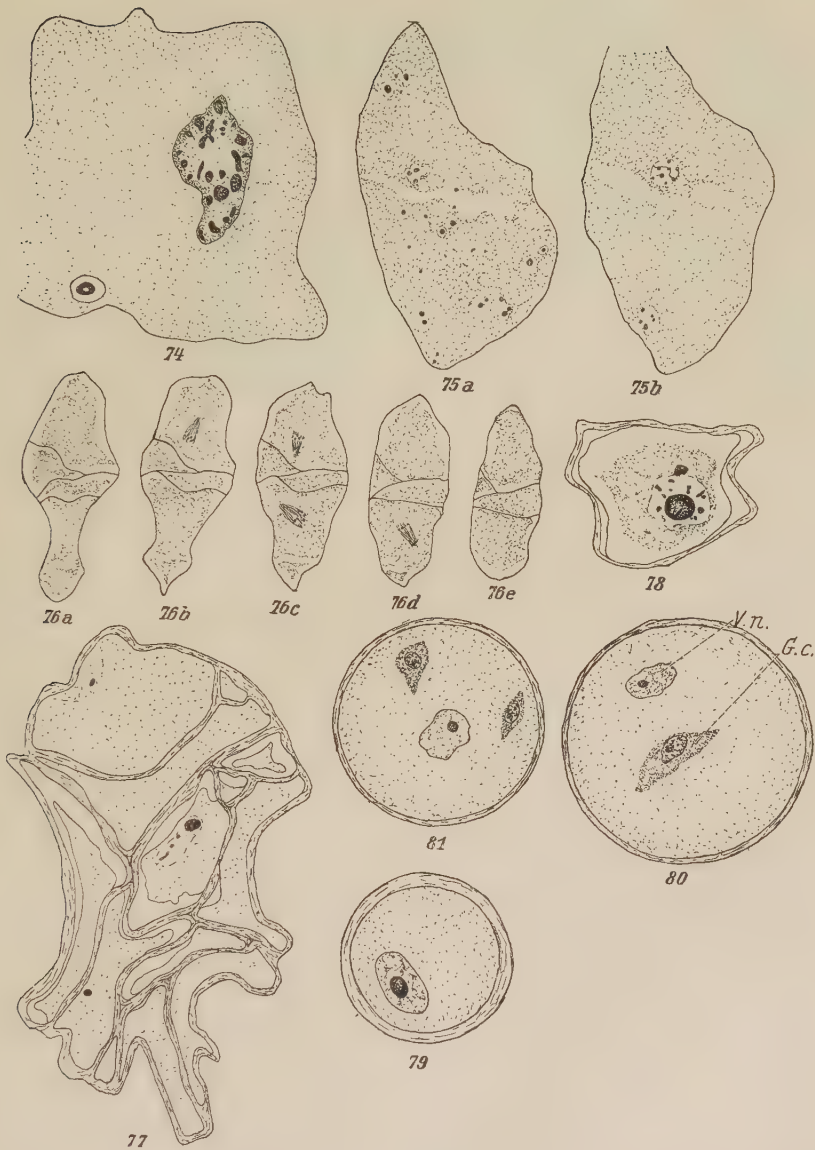
With the completion of the anaphase and during the reorganization of the daughter nuclei a definite wall is laid down on the spindle. The daughter nuclei pass through a brief interkinetic phase before the forma-



Figs. 66-73. Fig. 66. Pollen mother cell, presynaptic stage. Prochromosomelike bodies are strikingly evident. $\times 1700$. — Fig. 67. Four sections of one *P. M. C.* showing the same bodies. $\times 500$. — Fig. 68. Nucleus of *P. M. C.* in synapsis (see text). $\times 1700$. — Fig. 69. Five sections (*a-e*) of a post synaptic nucleus with thirty-two chromosomes. $\times 900$. — Fig. 70. Three sections. Diakinesis. Not all chromosomes are closely paired. $\times 900$. — Fig. 71. Three sections showing 32 chromosomes. $\times 1700$. — Fig. 72. Three sections. Meiosis I. Eight chromosomes have lagged near the equator and show a median split, while twelve pairs have already separated. Such figures appear frequently. $\times 1700$. — Fig. 73. Polar view of Meiosis I showing sixteen chromosomes. $\times 1700$.

tion of the second meiotic spindles. These are commonly perpendicular to the first, but may lie in any plane whatever. Here again, the chromosomes, which now show distinctly the beginnings of the subsequent equational splittings, are sixteen in number in polar view. With the completion of this division walls are again laid down, forming the definitive microspores. These round off, the relatively thin pollen mother cell bursts, an exine is deposited about each one and thus the normal, uninucleate pollen grain, such as is illustrated in fig. 78, is formed.

The development outlined above is the closest approach to the normal that I have observed in the Gros Michel. The fact that D'ANGREMOND (2), TISCHLER (70), and COOPER (21) were all able to germinate a certain percentage of pollen grains, shows that such complete development must occur in part of the tetrads. Degeneration, however, may set in at any stage subsequent to diakinesis. As has been said, the chromosomes often lag on the first meiotic spindle. If, as is often the case, the reorganization of the nuclei begins before completion of the anaphasic movement, the various chromatin fragments are organized into separate karyomerites, sometimes one for each chromosome (fig. 75) (see TISCHLER, 70; BALLY, 5; TÄCKHOLM, 66, et. al.). As CHODAT (18) has pointed out from observations made *intra vitam* on the sporogenesis of *Allium ursinum*, these ordinarily fuse to form the mature interkinetic neucleus and no abnormality necessarily results. The irregular and pyriform nuclei found here such as that illustrated in fig. 74 clearly indicate that such fusions occur, and they are undoubtedly responsible for the figures which D'ANGREMOND (2) has interpreted as "amitotic". This also agrees with BALLY's observations on *Triticum*—*Aegilops* Hybrids (5) and with D'ANGREMOND's (2) and TISCHLER's (70) observations on *Musa*. However, just as in the embryo sac mother cells, the formation of walls takes place very irregularly and in many cases these karyomerites are prevented from fusing through the intercalation of walls. Moreover, cytokinesis is in many cases so completely divorced from karyokinesis that cytoplasm is cut off which contain no sign of nuclear material, and I have observed "tetrads" of as many as twenty cytoplasm. In spite of the alteration in the nuclear-plasma ratio, which occurs through the introduction of such supernumerary walls, the second meiotic spindle is generally formed. It is, however, often badly distorted and pushed aside (fig. 76). I have not observed the formation of supernumerary spindles such as are described by BALLY (5) and TÄCKHOLM (66) so that it seems probable that wherever karyokinesis occurs it goes on normally. The final result of all this abnormality in the behaviour of both tapetum and archesporium is the complete degeneration of the vast majority of the potential microspores in this variety. Most of the parthenocarpic varieties of *Musa* behave in like manner (see Part III).



Figs. 74-81. Fig. 74. Nucleus incompletely organized after Meiosis I giving a suggestion of amitosis. A "sonderkern" below. $\times 1700$. — Fig. 75. A pollen mother cell with scattered "sonderkerne". $\times 500$. — Fig. 76. A pollen mother cell with Meiosis II spindles. Four walls have already been laid down. $\times 250$. — Fig. 77. A "tetrad" of twelve or more cells. $\times 500$. — Fig. 78. Nearly mature pollen grain. $\times 500$. — Figs. 79-81 are of the variety *Coolie Hongkseng*. Fig. 79. A pollen grain just after the dissolution of the P. M. C. wall. $\times 500$. — Fig. 80. Pollen grain 5 days before shedding with generative cell (G. c.) and vegetative nucleus (V. n.). $\times 500$. — Fig. 81. Pollen grain as in figure 80 but with two generative cells. $\times 500$.

Development of the Anthers, Rodoc Clamp¹.

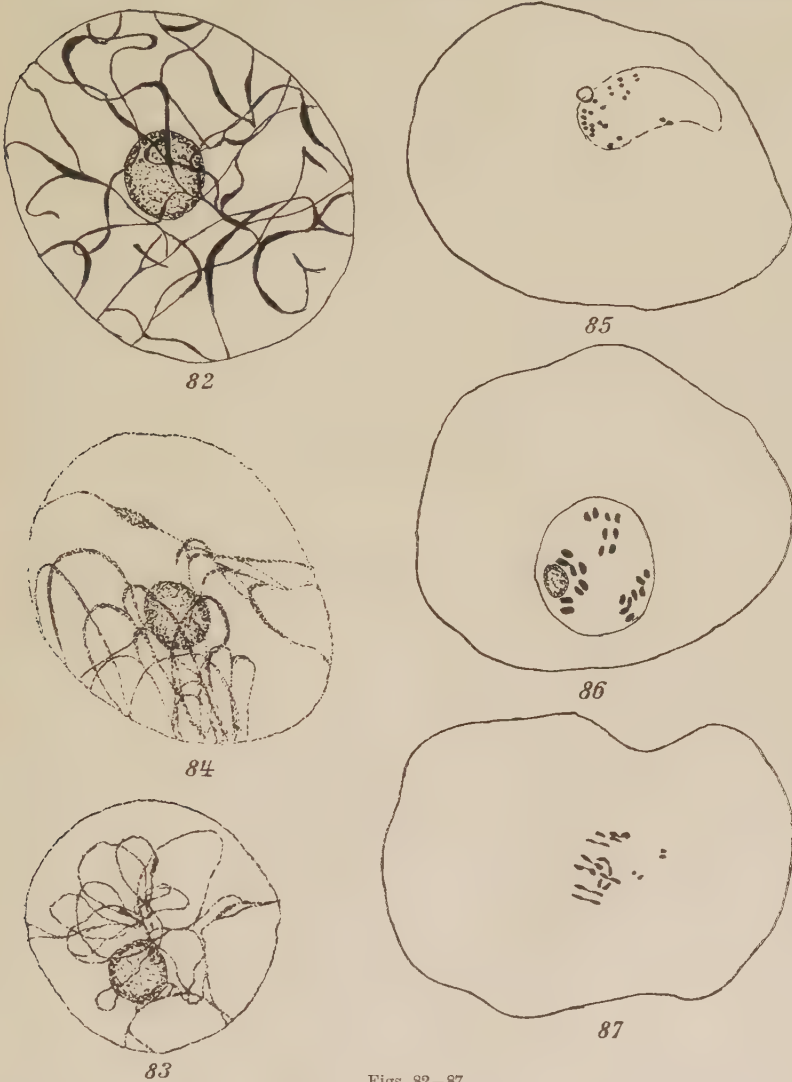
In the fertile-varieties, the development of the anthers goes on quite as in the more normal phases of the Gros Michel, up to diakinesis. The tapetum may degenerate *in situ* but no periplasmodium is formed and there is no secretion of slime although the anther may develop far beyond the size which the pollen mother cells can fill, leaving cavities between them. This variety has twenty-four chromosomes and at diakinesis all twelve diads are formed. Two of these diads often show a much less close union than do the others, but this is by no means universal. The diads themselves are often grouped in fours at three sides of the nucleus (fig. 86). At the final dissolution of the nuclear membrane the two diads mentioned above are at times somewhat separated from the rest and are consequently tardy in entering the equatorial plate (fig. 85) but once the plate is formed, division goes on entirely normally, twelve chromosomes passing to each pole. As in the Gros Michel, the dividing wall is laid down immediately, the nuclei pass to the homeotypic division and the tetrad is completed. It is commonly "four in a row" but may occasionally be tetrahedral. Intercallation of supernumerary walls often occurs even in these fertile varieties, resulting in an alteration of the nucleo-plasmic ratio and subsequently in a more or less considerable percentage of degenerating pollen.

After the breaking up of the tetrad the pollen grains round off and enlarge rapidly, a vacuole forms at the center of each and the protoplast takes up a periferal position, with the nucleus at one side. After the pollen grain has reached its full size, this vacuole gradually disappears. The nucleus divides (see D'ANGREMOND, 2) and one daughter nucleus returns to the center of the cell. This nucleus enlarges and loses its chromatic character becoming the vegetative nucleus. The other nucleus, the generative nucleus, lies next the wall of the microspore in a distinct mass of denser cytoplasm, which, however, is not cut off by a cell wall. The generative nucleus remains distinctly chromatic and elongates. Sometimes it divides even before the pollen is shed so that two spindle-shaped sperm nuclei are present along with the larger, spherical vegetative nucleus (fig. 81). The protoplast becomes filled with starch. The exine which is deposited on the pollen grains, is uniform in thickness throughout so that the pollen grains when shed are perfectly spherical and smooth. They may show a slightly flocculated surface, as if a coat of mucilage had dried on them and cracked, but there are no distinguishable germina-

¹ The fixed materials obtained for the study of this variety proved inferior in many cases to the smears made of related varieties according to the TAYLOR technique (67). I have therefore, in some cases, used drawings of other related varieties to supplement those made from Rodoc Clamp material. The stages represented are essentially the same as those to be found in the latter variety.

tion pores and the exine is so thin that the pollen cannot be exposed to the air for long without being dried out and killed.

Both TISCHLER (70) and D'ANGREMOND (2) found pollen grains ger-



Figs. 82-87.

Figures 82-84 are of the variety *Ta Ni Pa*. Fig. 82. Nucleus of pollen mother cell. Presynaptic, in living condition. $\times 2800$. — Fig. 83. Nucleus of *P. M. C.* in synapsis. $\times 2800$. — Fig. 84. A similar tangle seen from the edge showing the distinct "bouquet". $\times 2800$. — Fig. 85. Variety "Manang". Late prophase, just at the moment of dissolution of the membrane. Note the two dyads separated from the rest. $\times 1200$. — Fig. 86. Variety "Manang". Diakinesis showing three groups made up of four dyads each. $\times 1200$. — Fig. 87. Variety "Bolo". Twenty-four chromosomes at metaphase. $\times 1200$.

minating within the anther and COOPER (21) has shown this to be of common occurrence in most of the bananas, particularly the seedless varieties. Since there is no germinating pore in the exine, germination takes place by rupturing of this wall, apparently at any point. D'ANGREMOND (2) and COOPER (21) have studied the germination of pollen of a number of varieties on various media and have recorded rates of growth. The latter author reports very strikingly branched pollen tubes in certain varieties (notably "Green-Red") which he thinks may be in part responsible for the sterility of these varieties, the sperm nuclei being caught in blind branches. It is not certain, however, that such branched tubes occur in the stigmatic tissues as they do on artificial media.

Although we have, as we have seen, good reason for believing that the Gros Michel is a hybrid and that its sterility may be explained on this basis, we have also much evidence that this sterility is not absolute and that it may be possible to increase the fertility by artificial means. MICHEALIS (35) working with *Epilobium* and DE MOL (37) with *Malus* have shown that even in hybrids the degree of development of the spores and gametes may be altered by changes in temperature. LEWITSKI (32) has accomplished similar modifications in *Rumex* by the use of incisions at various points in the inflorescence. SAGOT (58) has observed that in Tahiti the fertility of *Musa Fehi* VIEILL is dependent upon the altitude at which it has been grown and many observations suggest that the adequacy of nutrition may play a part in the development of the reproductive parts. Although equipment was not available for detailed experiments a number of castrations of various sorts were performed on inflorescences to test these possibilities, in some cases as early as six weeks before their normal sexual maturity and hence just after the maturation of the definitive archesporia. From the results of these experiments it was evident that incisions, removal of male, female or neuter flowers or of any two of these, castrations, etc., have no effect upon the organs retained, at least unless performed before the differentiation of the definitive archesporia. It was not possible to alter the progress of the reduction divisions by any methods tried by me at Almirante. It is possible that this sort of study might be pushed further to advantage, but that is beyond the scope of the present paper.

Conclusions.

From the results so far gained, it is evident that although eggs and sperms, which are theoretically capable of functioning, are occasionally formed in the parthenocarpic bananas, our chances of combining them so as to obtain progeny are very remote. They are, in fact, approximately the same as an animal breeder would have of obtaining a progeny by breeding two mules. And even if by crossing the Gros Michel with an

immune variety we get one viable seed in 100,000 attempts—and we can hardly hope for a higher percentage of success than this — there is still only a remote chance of obtaining the combination of factors which give us the desirable characteristics of the Gros Michel, including parthenocarpy, together with the immunity which we desire.

If we assume immunity to depend on a single gene, parthenocarpy on a second and all of the fruit characters on a third, an assumption which is patently improbable, and we assume further all the desired characters to be dominant and both parents to be homozygous for each dominant pair, which is also very improbable in plants of as mixed an origin as the bananas appear to be, we should get the combination we wish in every successful cross. If on the other hand these parents were in each case heterozygous for the dominant genes, our chances of success would be 1 : 8. Moreover, if the desired characters were recessive and the parents homozygous, we could never possibly obtain the desired combination in the first cross, and if the parents were heterozygous for the wanted characters, the chances of combining all three characters would be 1 : 8. We have, then, at most one chance in 100,000 of obtaining an immune Gros Michel by such breeding and the probability is certainly much less even than this figure¹.

But the stock breeder does not attempt to improve his mules by breeding them with other strains. Instead, he makes selections from progenies obtained from the same parents that produced his most efficient mules, that is from the progenies of selected mares and asses. If we can determine what were the parents of the Gros Michel banana, we should be able to do the same.

As we have already seen the chromosome complement of the Gros Michel is made up of thirty-two units, which at meiosis fall into two distinct groups, twenty-four bivalents, that is, twelve diads, and eight unpaired univalents. In examining into the origin of this compound complement, we have to consider a number of possibilities.

1. The simplest and most probable way in which such a complement might arise is by crossing one parent having twelve chromosomes (haploid) with another having twenty chromosomes. In this case, twelve of the twenty may be supposed to pair with the twelve chromosomes of the other parent, leaving the remaining eight unpaired. In this, the so-called "*Drosera* Type" of association (see SHARP, 62), it has been assumed that all of the chromosomes of the parent having the smaller chromosome number have their homologues among the chromosomes of the other parent, and that no two of the remaining eight chromosomes are homologous. This is probably the commonest type of chromosome association

¹ I am indebted to Professor H. S. JENNINGS for advice in preparing this paragraph and for criticism of Parts III and IV of this paper.

in hybrids and is represented in plants by such examples as *Drosera* (ROSENBERG, 55), *Triticum* (SAX, 59), *Rosa* (TÄCKHOLM, 66), etc.

The same result would be obtained if the original parent had been the result of crossing a six chromosomed (haploid) race with a ten chromosomed race followed by a doubling of the chromosome number as has been observed by ROSENBERG (57) and NAWASCHIN (40), or if it had come from a cross between a three-chromosomed (haploid) race and a five chromosomed race followed by a quadrupling of the chromosome number.

2. The only other possible origins for such a complement would require the occurrence of autosyndesis (see SHARP, 62), which is not indicated by the conditions observable at meiosis. We are thus led to search first for races of bananas having the somatic chromosome numbers twenty-four and forty and secondly for the numbers six, ten, twelve and twenty, although we have less evidence of the existence of these latter numbers than of the former. The third section of this paper will be devoted to the results of a search for these races.

PART III.

Comparative Karyology of the Genus *Musa*.

As has already been pointed out in Part II of this contribution, we have been led to search for strains, in this case species, in the Genus *Musa* having twenty-four and forty chromosomes as their respective diploid complements. TISCHLER (70) has counted eight in the haploid phase (16 diploid) of the clone "Dole", sixteen (32 diploid) in the clone "Rajah Siam" and twenty-four (48 diploid) for the clone "Pisang Kladi". He considers these all as varieties of *M. paradisiaca* L. subsp. *sapientum*. D'ANGREMOND (2) finds 12 chromosomes (24 diploid) in the species *M. basjoo* SIEB. et ZUCC., which thus may possibly be one of the two strains for which we are searching. These, however, tell us nothing of the other hypothetical parent and give us nothing like a comprehensive view of the genus *Musa* as a whole. It seemed necessary, therefore, to examine as wide a variety of material as could be obtained. Fortunately the United Fruit Company has gathered together, as a basis for future investigation, a collection of approximately two hundred clones from all parts of the world. It is to be regretted, from the point of view of the present study, that this collection was made with only the first program, that of improving varieties of already recognized commercial value, suggested in Part I, in mind. It is hence made up largely, not of a diversity of species and varieties, but of clones which at present show evident combinations of commercially desirable characteristics, many of them very closely allied, or even duplicate, strains coming from different regions of the

earth and passing under different names. There are as we shall see comparatively few of these which are likely to prove available as breeding stocks in our second program. The collection is, however, by far the most comprehensive available anywhere in the world today, as the once fine collection at Manila has been allowed to "run-down" since the hurricane of some years ago. It is to be hoped that the United Fruit Company's collection will, in the near future, be augmented in a more systematic way in the light of the present studies.

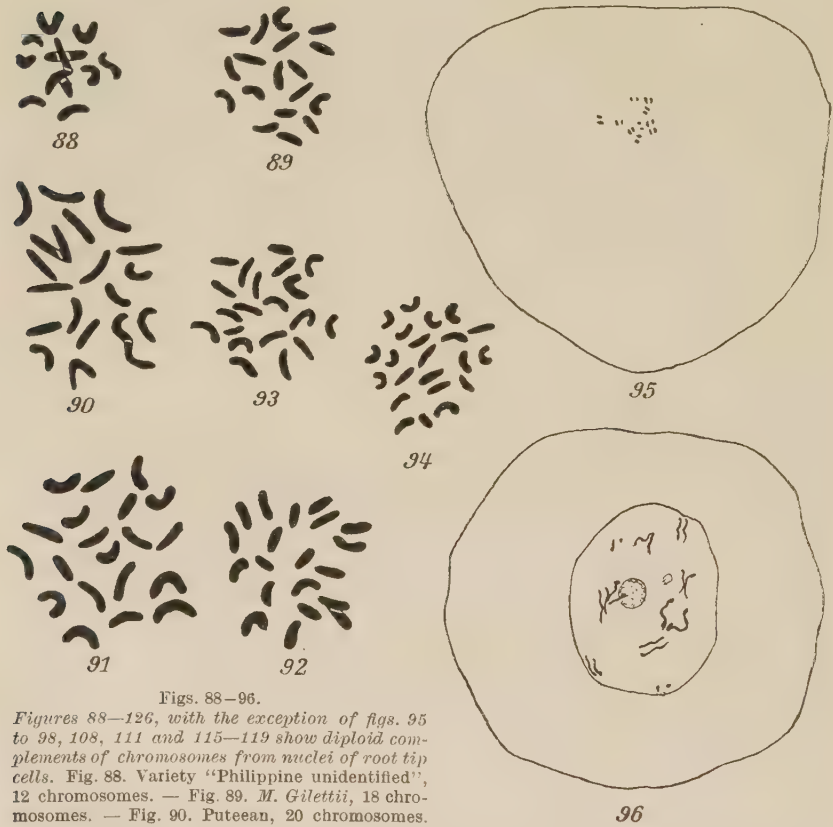
Such a karyological study may be conducted either (1) on somatic tissues or (2) on the meiotic phases. In most of the studies of this sort in the past the latter program has been followed. In view, however, of the irregularities which often tend to confuse the results in studies on the heterotypic and homeotypic divisions such as an-euploid distributions, fragmentation of chromosomes, etc., it has seemed to me better to use the somatic counts as the basis for my interpretations and to employ meiotic counts merely as a check on the manner of pairing of chromosomes. For this survey, only transverse sections of the root-tips of actively growing plants have been used.

A preliminary examination was made of collections obtained in the New York Botanical Garden in November, 1926. For these I have to thank Dr. N. L. BRITTON, Director-in-Chief of the Garden and Dr. A. B. STOUT, Director of the Laboratories. These were fixed in medium chrom-acetic, NAWASCHIN's fluid, NĚMEC's fluid, CHAMBERLAIN's modified formal-acetic alcohol, and CARNOY's fluid, both with and without chloroform. Both the CARNOY fluids caused such shrinkage as to be quite useless for this material. NĚMEC's fluid fixed the plastids and plastid primordia excellently but gave no nuclear differentiation. The NAWASCHIN's fluid gave excellent cytoplasmic and nuclear fixation but did not allow satisfactory differentiation under iron-alum of the nuclear details. Both medium chrom-acetic and formol-acetic fluids gave excellent results. The latter method is far easier, however, as no washing is required, material so fixed can be transferred at any time directly to 60% alcohol, and is not damaged if left in the fixative itself for months. Hence, it was chosen for all later collections. Root tips of one hundred and sixty clones¹ and a number of hybrids of recorded parentage were collected for me by Mr. J. H. PERMAR at Almirante. For preliminary study collections were made at 6 A.M., 10 A.M., 2 P.M., 6 P.M., and 10 P.M. None of these gave the desired number of mitotic figures and later collections were made at 2 A.M. with more satisfactory results. All sections were cut at 5μ in thickness and counts were made only from polar views of equatorial plates in metaphase or from anaphases in which

¹ The plants from India and Hawaii growing at Almirante in 1927 were not mature enough to be used in this study.

all of both sets of chromosomes could be counted in the two proper optical sections. No count has been accepted from less than three clear examples and where there was any doubt whatever repeated counts were made from several slides.

As a further check on the results of these somatic counts, smears were made of pollen mother cells before and during meiosis, using a modifica-



Figs. 88-96.

Figures 88-126, with the exception of figs. 95 to 98, 108, 111 and 115-119 show diploid complements of chromosomes from nuclei of root tip cells. Fig. 88. Variety "Philippine unidentified", 12 chromosomes. — Fig. 89. *M. Gilettii*, 18 chromosomes. — Fig. 90. Puteean, 20 chromosomes.

These are much longer and straighter than in most varieties. — Fig. 91. Bungulanon (*M. textilis*), 20 chromosomes. — Fig. 92. *M. ensete*, 20 chromosomes. — Fig. 93. Kababar A, 20 chromosomes. — Fig. 94. Sinaba (*M. textilis*), 20 chromosomes. — Fig. 95. Bungulanon (*M. textilis*) Meiosis I, metaphase, 20 chromosomes. — Fig. 96. Bungulanon.

Diakinesis showing the dyads more elongated than in most varieties.

tion of TAYLOR's (67) technique. Aceto-carminé according to BELLING (6) and aceto-gentian were tried but without success and even the TAYLOR technique gave only indifferent results. These have been set down only where the results seemed sufficiently clear to warrant their acceptance.

This investigation has given me an excellent polyploid series ranging from twelve to forty-eight. For reasons which will appear later, however, I regard the basic diploid number, as being not twelve, but eight. I have employed the terms triploid, tetraploid, etc., as they are used by BLACKBURN and HARRISON (9), ROSENBERG (55, 56), TÄCKHOLM (66), etc., i. e., as referring to chromosome *number* only and not to the number of known homologues present as do BLAKESLEE and BELLING (10). The results of this part of this study are set forth below.

Diploid ($2n$) = 8.

Although I am convinced that the basic diploid number for the genus *Musa* is eight, I have not as yet found any race having that number. If CLAUSEN's (19) ideas concerning the origin of plant genera by hybridization are valid, this number may perhaps not exist in *Musa* itself, but be found in some other genus of the Musaceae from which *Musa* has been derived. An examination of other genera, particularly *Heliconia* and *Strelitzia* might bring out interesting results. For the present, the assumed diploid number in *Musa* is purely hypothetical and we are only justified in assuming its existence by indirect evidence which we shall examine later.

Triploid ($3n$) = 12.

Of all the types of *Musa* available to me, only a single clone has shown the triploid number, twelve. This is an unidentified variety from the Philippines, which shows many resemblances to both *Musa basjoo* (24) and *M. seminifera* (24). It should prove worth further investigation (fig. 88).

Tetraploid ($4n$) = 16.

I have not found the tetraploid number in any of the clones which I have examined. TISCHLER (10), however, working on the reduction divisions, has reported this number in a clone from Amani, Tanganyika Province, East Africa, which is known as "Dole". I have been unable to obtain any detailed information concerning this clone or to get material of it for study. It is to be hoped that other tetraploid varieties will be found.

With the exception of *M. Gilletti* and *M. ensete*, which belong to the subgenus *Physocaulis* and *M. glauca* which is a transition form between *Physocaulis* and *Eumusa* these clones probably all belong to *M. textilis*. This species certainly has its highest development and probably its center of distribution in the Philippines. It seems probable that pentaploid races have arisen separately in the two subgenera, in *Eumusa* in the far East, and in *Physocaulis* in the west, perhaps even in South America (see Part I). The members of the two subgenera bear little resemblance to one another. The presence of the number 18 in *M. Gilletti*, a number

Pentaploid (5n) = 20.

Serial ¹ No.	Species	Varietal Name ²	Originating from ²	Chromo- some number	Pollen Class ³
1	<i>M. glauca</i> . .	Virgin	India	?	A?
2	—	Nandou	Wasier, Wainami,	20	—
		Kabebar (A)	New Guinea		
28	—	Bayalang	Philippines	20	—
29	<i>M. Gilletti</i> . .	—	—	18(?)	—
31	<i>M. ensete</i> . . .	Abyssinian	Abyssinia	20	—
207	<i>M. textilis</i> . .	Maguindanao	Philippines	20	—
208	" " . .	Bungulanon	"	20 ^a	—
209	" " . .	Tangongon	"	20 ^a	—
210	" " . .	Puteean	"	20	—
212	" " . .	Sinaba	"	22(?)	—
215	" " . .	Libuton	"	20	—

which does not occur anywhere in the *Eumusae* further supports the idea of a separate evolution within the two groups and it seems quite probable that a closer examination of *Physocaulis* would reveal a very different series from that to be found in *Eumusa* (figs. 89—96).

Hexaploid (6n) = 24.

Serial No.	Species	Varietal Name	Originating from	Chromo- some number	Pollen Class
2	—	Bastard Hemp	Philippines	24	A
3	<i>M. basjoo</i> . . .	Martini	(Farther India)		
			Philippines	24	A
4	" " . . .	Alisanag	"	24	A
5	" " (?) . .	Rodoc Clamp	"	24	A
7	—	Coolie			
		Hongkseng	"	24	A
8	—	Kacoloan	"	24	A
9	—	Yale Bale	"	24	A
10	—	(Unid)			
		Sanderson's	Panama	24	A

¹ These are the numbers which have been used in the planting and breeding records at Almirante.

² See note 1, p. 679.

³ I am indebted to Mr. G. P. COOPER for permission to use these figures which are to be found in his report (21). Class A is 20—100% germination, Class B, 5—20%, Class C, 1—5% and Class D under 1% germination.

^a Meiotic combination $\frac{16 + 24}{2} = 20$.

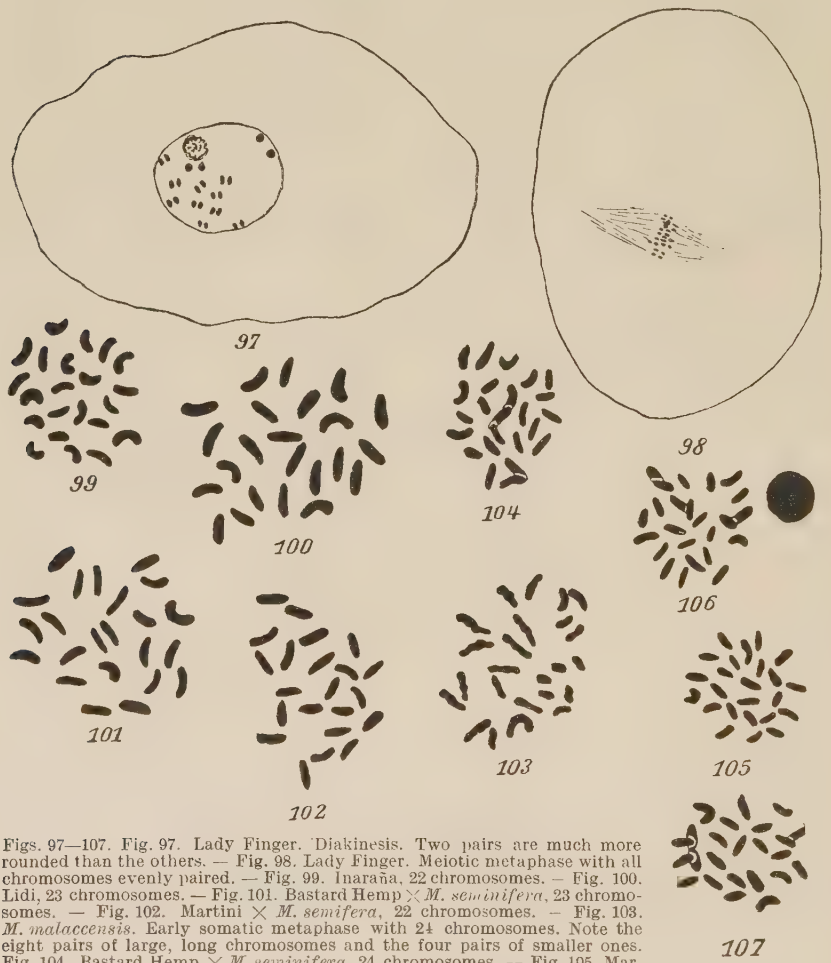
Hexaploid (6n) = 24 (continuation).

Serial No.	Species	Varietal Name	Originating from	Chromosome number	Pollen Class
11	—	Bolo	Philippines	24	B
12	<i>M. paradisiaca</i> .	seminifera	Burma	24	—
14	<i>M. Cliffortiana</i>	asperma	„	24	—
15	<i>M. Crachycarpa</i>	Back. ‡ 72	Java	24	—
16	<i>M. Zebrina</i> . .	cerifera	Malacca	24	—
17	<i>M. Zebrina</i> . .	—	„	24	—
18	<i>M. sanguinea</i> .		Farther India	24	—
19	<i>M. acuminata</i> .	Simiarum	Java	22(?)	C
20	<i>M. rosacea</i> . .		Burma, Java	24	—
23	—	Nandou	New Guinea	24	—
		Kabebbar (B)			
25	—	Pisang Kawahi (Tobelo)	Halmaheira, Dutch E. Indies	24	—
26	—	Pisang Kawahi (Galela)	„ „ „	24	—
30	—	Pacol	Philippines	24	—
32	<i>M. paradisiaca</i> .	Martabon	„	24	—
		Dacca			
57	<i>M. basjoo</i> . . .	Manang	„	24	B
60	<i>M. basjoo</i> (?) .	Lidi	Sumatra	23	B
63	—	Klui Kran	Siam	24	B
64	—	Djantan	Sumatra	24	D
116	—	Lady Finger	Panama	24 ^b	B
121	—	Viente Cohol	Philippines	24	D
122	—	Putian	„	24	D
123	—	Galimba Pula	„	24	D
144	—	Inarnibal	„	24	C
145	—	Chek Pong Man	Fr. Indo-China	24	B
		Pluc			
146	—	Chuoï Cau	„ „ „	24	B
		Trang			
155	—	Sinaroksok	Philippines	24	—
166	—	Morong Datu	„	24	D
169	—	Pulutan	„	24	D
170	—	‡ 20 Mundan	Federated Malay States	24	D
175	—	Sabang Tagolog	Philippines	24	D
191	—	Chuoï Tien			
		Huong	Fr. Indo-China	24	D
194	—	Inaraña	Philippines	22(?)	—
—	—	Pisang Pandok	Java	24	—
		Beureum			

^b Meiotic combination $\frac{16 + 16 + 16}{2} = 24$.

Hexaploid (6n) = 24 (continuation).

Serial No.	Species	Varietal Name	Originating from	Chromosome number	Pollen Class
	Hybrid . . .	Bastard Hemp × seminifera	(B. H. type	24	
	" . . .	Bastard Hemp × seminifera	(Distinct type)	23	
	" . . .	Alisanag × seminifera	(Sem. type)	24	
	" . . .	Martini × seminifera	(Mart. type)	24	
	" . . .	Martini × seminifera	(Sem. type	22	



Figs. 97—107. Fig. 97. Lady Finger. Diakinesis. Two pairs are much more rounded than the others. — Fig. 98. Lady Finger. Meiotic metaphase with all chromosomes evenly paired. — Fig. 99. Inaraña, 22 chromosomes. — Fig. 100. Lidi, 23 chromosomes. — Fig. 101. Bastard Hemp × *M. seminifera*, 23 chromosomes. — Fig. 102. Martini × *M. seminifera*, 22 chromosomes. — Fig. 103. *M. malaccensis*. Early somatic metaphase with 24 chromosomes. Note the eight pairs of large, long chromosomes and the four pairs of smaller ones. Fig. 104. Bastard Hemp × *M. seminifera*, 24 chromosomes. — Fig. 105. Martini × *M. seminifera*, 24 chromosomes. — Fig. 106. Rodoc Clamp, 24 chromosomes. The nucleolus is still intact. — Fig. 107. Rodoc Clamp, 24 chromosomes.

The hexaploid series is restricted to the Eumusae and includes nine recognized species centering around Farther India and Malaya proper. Many, if not all, of the twenty clones originating from the Philippines are varieties of *Musa basjoo*, which is found wild in Farther India. It seems probable, therefore, that they are of recent introduction in these islands. On the other hand *M. seminiifera*, *M. zebrina*, *M. sanguinea*, etc., are well defined species and seem likely to have sprung from much more ancient stocks (figs. 97—107).

Septaploid ($7n$) = 28.

I have found only a single established clone which is septaploid, the "Dorado", which is from Cuba, but of unknown primary origin. Its pollen is of Class D and it is not an especially outstanding type in anyway. We have, however, another clone, known to be a cross between Apple Plantain (32) and Bastard Hemp (24) (Bastard Hemp Type) which is septaploid. This gives us an indication of how these odd-multiple counts may have been derived. The pollen of class D, in "Dorado" is what we should expect from an unbalanced polyploid (see BLACKBURN and HARRISON, 9). It is interesting to note that this is the same cross as that which supposedly gave rise to the "DUNLAP's Seedling" which will be discussed later (figs. 108—109).

Octoploid ($8n$) = 32.

Serial No.	Species	Varietal from	Originating from	Chromosome number	Pollen Class
13	—	Ta Ni Pa	Siam	32 ^c	A
21	—	Butuan	Philippines	32	—
51	<i>M. paradisiaca</i>	Chamaluco			
		Apple plantain	Cuba	32	—
52	" "	Cenizo	"	32	—
		Apple plantain			
53	" "	Burro	"	32	D
		Apple plantain			
54	" "	Guyuran	Philippines	32	D
55	" "	Red	Panama	32	C
56	<i>M. paradisiaca</i>	Green Red	"	32	C
62	—	Kalibo	Philippines	32	D
66	—	Masak Sahari	Sumatra	32	D
67	—	Nandou Mamboef Diodi	New Guinea	32	—

$$\text{Meiotic combination } \frac{32 + 32}{2} = 32.$$

Octoploid (8n) = 32 (continuation).

Serial No.	Species	Varietal Name	Originating from	Chromosome number	Pollen Class
102	<i>M. paradisiaca</i>	Gros Michel	Panama	32 ^a	D
103	" "	" "	Venezuela	32	D
104	" "	" "(?)	Sierra Leone	32	D
105	" "	Lacatan	Panama	32	C
106	" "	" (?)	Sierra Leone	32	D
107	" "	"	Philippines	32	D
108	" "	Congo	Panama	32	C
112	" "	Giant Fig	Grenada (W. I.)	32	D
114	<i>M. Cavandishii</i> . . .	Bungulan (Tumoc)	Philippines	32	D
115	—	Tadio	"	32	D
117	—	Bat Nose	Panama	32	D
118	—	Guineo Prieto	"	32	D
124	<i>M. Cavandishii</i> . . .	Chinese	"	32	D
125	<i>M. paradisiaca</i> . . .	Maiden Plant.	"	32	—
126	" "	Blackstemmed Maiden Plant.	"	32	—
128	" "	Horse Plantain	"	32	—
129	" "	Black stemmed Horse Plantain	"	32	—
130	" "	Red Plantain	"	32	—
131	" "	Dwarf Horse Plant.	"	32	—
132	" "	Indio Plantain	"	32	—
137	—	Chuoi Gia Huong	Fr. Indo-China	32	D
140	—	Baloko	Philippines	32	D
141	—	Morado Puti	"	32	D
142	—	Morado Pula	"	32	D
143	—	Morong Principe	"	32	D
147	—	Pomme Java	Fr. Indo-China	32	D
148	—	Manzana	Colombia	32	D
151	—	Martinique	Martinique	32	D
152	—	Chuoi Cha	Fr. Indo-China	32	D
156	—	Raja	Federated Malay States	32	D
157	—	Kapas	Federated Malay States	32	C
158	—	Pisang Cocos	Batjan, Dutch E. Indies	32	—

$$\text{Meiotic combination } \frac{32+32}{2} = 32.$$

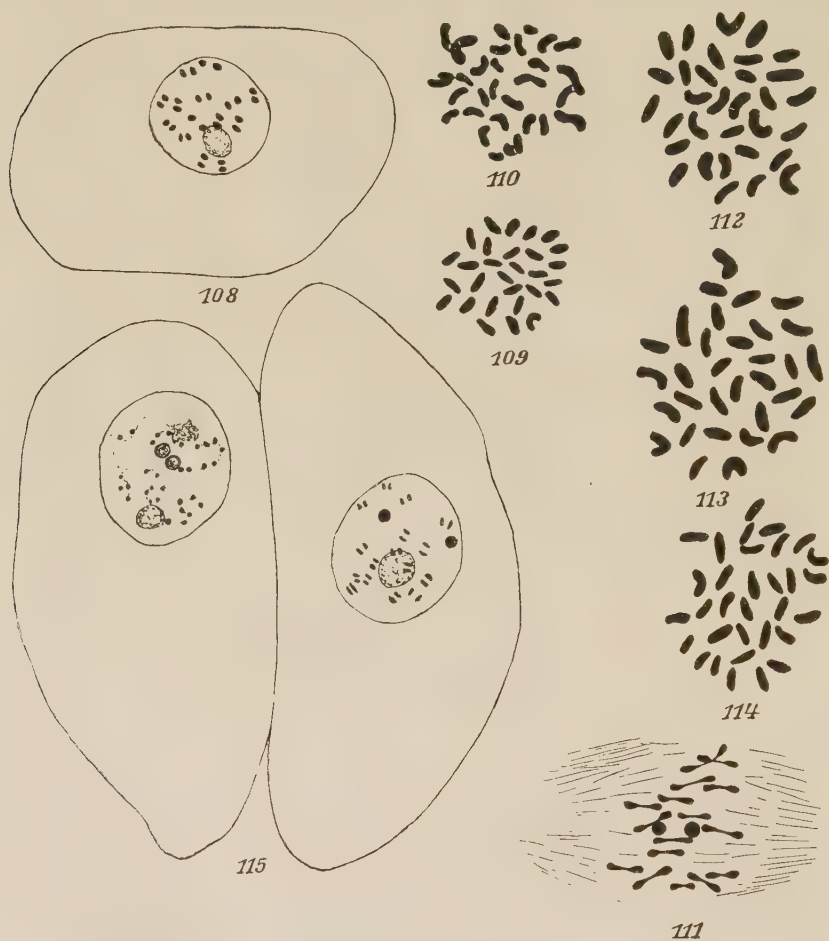
$$^a \text{ Meiotic combination } \frac{40+24}{2} = 32.$$

Octoploid (8n) = 32 (continuation).

Serial No.	Species	Varietal Name	Originating from	Chromosome number	Pollen Class
159	—	Pisang Boeloei	Halmaheira, Dutch E. Indies	32	—
162	—	Vi-ma-ma	Australia, Fijis	32	—
168	—	Six-A	Panama	32	—
171	—	Serendeh	Federated Malay States	32	C D
172	<i>M. Cavendishii</i>	Poot	Philippines	32	—
173	—	Tudoc	"	32	D
176	—	Decosta White	"	32	D
177	—	(Unid.)	Fr. Indo-China	32	D
181	—	Valery	" " "	32	D
182	—	Chek Ambong Plok	" " "	32	D
183	—	Chek Ambong Sneng	" " "	32	— D
185	—	(Unid.)	Porto Rico	32	—
188	—	Ambong Koerik	Sumatra	32	D D
192	<i>M. paradisiaca</i>	Black stemmed Gros Michel		32	—
193	" " (?)	F. H. B. 57246	Fiji	32	—
201	—	Pisang Galipapo	Halmaheira, Dutch E. Indies	32	—
	Hybrid . . .	Apple plant. × Bastard Hemp	Panama	32	—

The fifty-nine clones which fall in this group are all variations of *M. paradisiaca* or of its near relatives with the probable exception of Ta Ni Pa, and show a much greater variability in external characters and a wider distribution than does any of the previous groups. As we have already shown (Part II) this group is made up for the most part of one or more hybrid series resulting from a hexaploid-decaploid cross, and hence "unbalanced" octoploids (TÄCKHOLM, 66). Ta Ni Pa, however, stands apart from the rest in having highly fertile (Class A) pollen. I have not been able to examine the meiotic phenomena of this variety in detail, but the meiotic behaviour of some other varieties with Class C pollen or better, such as Apple plantain, Green Red, etc., indicates a balanced or eu-octoploid constitution in these strains. Such a constitution might result either by doubling of a tetraploid or else by balancing of a previous triploid-pentaploid cross by doubling. The latter process seems unlikely since we have found only a single triploid strain which originated from

the Philippines, a region in which it seems improbable that *M. paradisiaca* subsp. *normalis* could have arisen. Ta Ni Pa seems almost certainly to be such a balanced octoploid. The indigenous octoploids are concen-



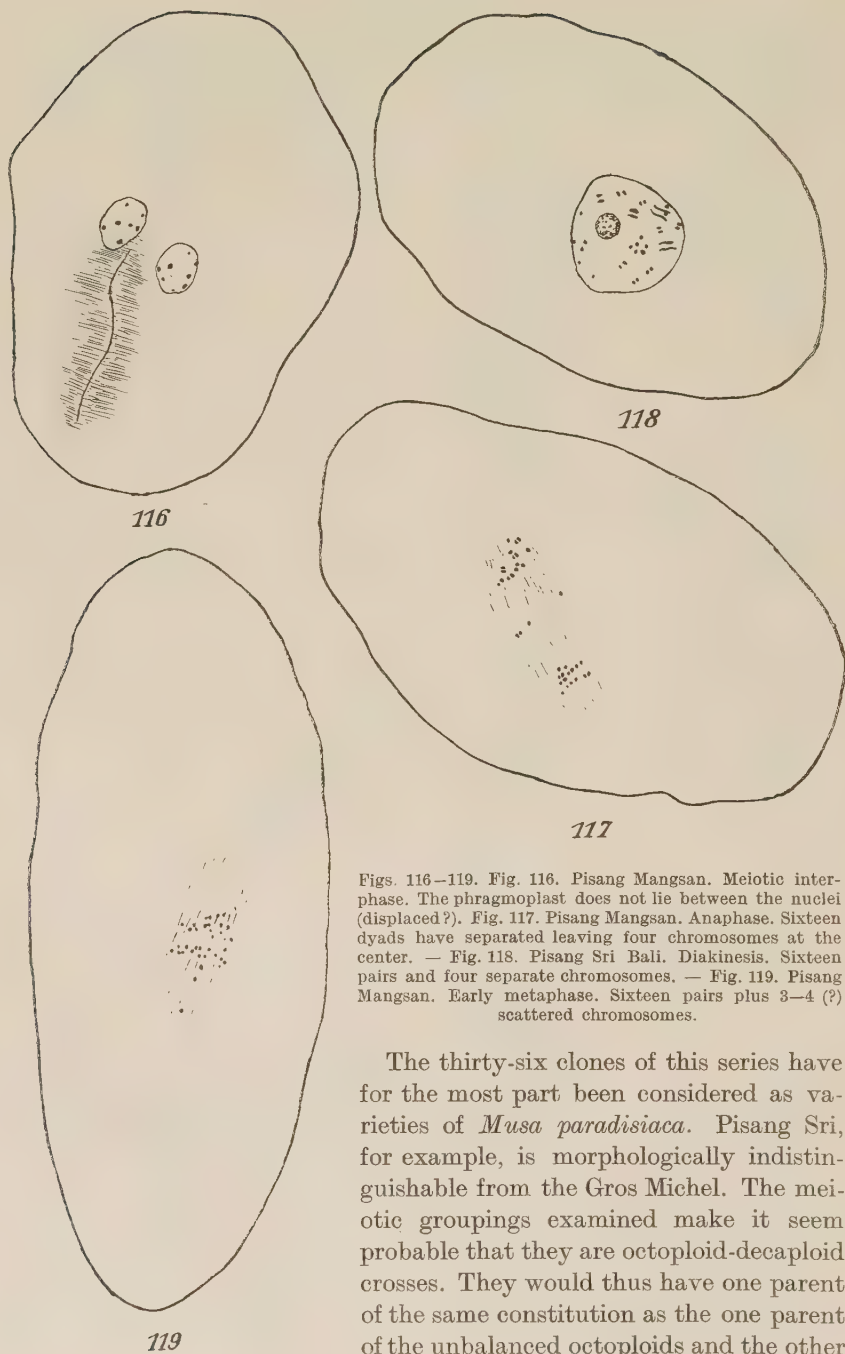
Figs. 108—115. Fig. 108. Dorado. Diakinesis. Fourteen dyads. — Fig. 109. Dorado, 28 chromosomes. — Fig. 110. Ta Ni Pa, 32 chromosomes. — Fig. 111. Indio Plantain. Meiotic metaphase with 16 pairs of chromosomes. Note the two small nucleoli in this and in fig. 115. — Fig. 112. Gros Michel, 32 chromosomes. — Fig. 113. Indio Plantain, 32 chromosomes. — Fig. 114. 'Apple Plantain' $\times$ Bastard Hemp, 32 chromosomes. — Fig. 115. Indio Plantain. Diakinesis and early metaphase, 32 chromosomes. Note the nucleoli.

trated around northern India, Farther India, Malaysia and Siam, but have been scattered artificially far too much to allow us to hope to locate their original center of distribution. It seems almost certain that the whole series of octoploids represent a number of parallel lines of evolution (figs. 110—115).

Nonoploids (9n) = 36.

Serial No.	Species	Varietal Name	Originating from	Chromosome number	Pollen Class
59	—	Kelat	Federated Malay States	36	C
61	—	Rotan	Sumatra	36	D
65	—	Kale	"	36	D
111	—	Bumulan	Panama	36	D
113	—	Bluefield	Hawaii	36	D
118	—	Brazilian	"	36	D
133	—	Bangalan †† 1	Philippines	36	D
136	—	Klui Hom Keo	Siam	36	D
138	—	Masak Hijau	Federated Malay States	36	D
139	—	Embun	"	36	—
149	—	Chuoi Cau Tay	Fr. Indo-China	36	—
150	—	Chevalier	" " "	36	—
153	—	Chek Tuk	" " "	36	D
154	—	Kanara	Philippines	36	—
160	—	Susu	Federated Malay States	36	D
163	—	Tandoek	Sumatra	36	D
		Kambing			
164	—	Pisang Sri	Java	36	D
165	—	Pisang	Malacca	36	—
		Seroeanota			
175	—	Sabang Castila	Philippines	36	—
178	—	Pisang Sangate	Halmaheira	36	—
			Dutch E. Indies		
179	—	Chuoi Gia Cui	Fr. Indo-China	36	D
180	—	" Cau Xiem	" " "	36	D
184	—	(Unid.)	Cook Islands	36	D
		Vi-ma-ma type			
186	—	Pisang Mangsan	Java	36	D
187	—	Chuoi Gia Lung	Fr. Indo-China	36	—
189	—	Pisang Ambon	Java	36	—
		Loemoet			
190	—	Pisang Masan	"	36	—
195	—	Laknau	Philippines	36	C
196	—	Pisang Ambon	Java	36	D
		Poetih			
197	—	Pisang Sri Bali	"	36	D
198	—	Nand. Aboeboe	New Guinea	36	—
200	—	" Kabaker	" "	36	—
204	—	The Hmwe	Burma	36	—
206	—	Amrita Sogar	India	36	—
		Coll. †† 106		36	—
		" †† 111		36	—

$$\text{Meiotic combination } \frac{32 + 40}{2} = 36.$$



Figs. 116–119. Fig. 116. Pisang Mangsan. Meiotic interphase. The phragmoplast does not lie between the nuclei (displaced?). Fig. 117. Pisang Mangsan. Anaphase. Sixteen dyads have separated leaving four chromosomes at the center. — Fig. 118. Pisang Sri Bali. Diakinesis. Sixteen pairs and four separate chromosomes. — Fig. 119. Pisang Mangsan. Early metaphase. Sixteen pairs plus 3–4 (?) scattered chromosomes.

The thirty-six clones of this series have for the most part been considered as varieties of *Musa paradisiaca*. Pisang Sri, for example, is morphologically indistinguishable from the Gros Michel. The meiotic groupings examined make it seem probable that they are octoploid-decaploid crosses. They would thus have one parent of the same constitution as the one parent of the unbalanced octoploids and the other

parent would itself be octoploid. It is therefore not surprising that members of the same phenotype should occur in these two groups. Their wide and sparse distribution indicate either a multiple origin or recent introduction (figs. 116—123).

Decaploid ($10n$) = 40.

Serial No.	Species	Varietal Name	Originating from	Chromosome number	Pollen Class
24	—	Tiparot	Philippines	40	—
58	Hybrid	Dunlap's Seedling	Panama	40 ^c	B



Figs. 120—126. Fig. 120. Kabaker, 34 chromosomes. — Fig. 121. Chevalier, 36 chromosomes. — Fig. 122. Pisang Mangsan, 36 chromosomes. — Fig. 123. Nandou Babekar (B). A cell with double complement (46 chromosomes). The neighboring cells have 24 chromosomes. — Fig. 124. Tiparot, 40 chromosomes. — Fig. 125. Dunlap's seedling, 40 chromosomes. — Fig. 126. Morado Puti. A cell with double complement (61 chromosomes). Neighboring cells have only 32 chromosomes.

Unless we assume the functioning of diploid gametes (apospory) and assign as one of the parents of our octoploid and nonoploid races the pentaploids, we must assume the existence of decaploids. I was therefore much pleased to find among the last varieties examined, these two decaploid clones. Tiparot is a banana from the Philippines, whose morphology is unknown to me. The DUNLAP'S Seedling, however, is better known. It was a chance seedling out of Apple Plantain, one of the rarely-seeded octoploid clones. Since, throughout the genus *Musa* the male portion of the inflorescence does not appear until much later than

^c Meiotic combination $\frac{32 + 24 + 24}{2} = 40$.

the female, this seed could not have been the result of selfing. The only varieties in the neighborhood available as pollen parents were clones of the hexaploid Bastard Hemp group. Theoretically such an octoploid-hexaploid cross should have given a septaploid with twenty-eight chromosomes. The appearance of a decaploid from such a cross is therefore of great interest. It can be explained only by assuming that a hexaploid (diploid) pollen grain had fertilized a normal tetraploid (haploid) egg. Observations on the pollen mother cells suggest that such diploid pollen grains may be formed in both pentaploids and hexaploids (possibly in other series as well) and it is possible that only such microspores are functional (compare ROSENBERG, 57 and NAWASCHIN, 40). This gives a new importance to the hexaploids, in our scheme, since they may function as dodecaploids. It is especially interesting to note that this clone falls in pollen class B with as high as twenty per cent germination, in spite of the fact that it has a very high chromosome number and is not theoretically an especially well balanced combination. A study of its meiotic behaviour should prove very interesting (figs. 124—125).

Ondecaploid ($11n$) = 44.

I have not encountered this number anywhere in the material examined and since it would necessarily be an especially unbalanced combination it would be surprising if it had ever persisted. This one gap in the polyploid series is thus not surprising. (Compare the rarity of the triploids and septaploids. The persistence of the pentaploid over these may be explained in several ways. See Part IV.)

Dodecaploid ($12n$) = 48.

As with the tetraploid series, I have not, myself, encountered this number but must refer to TISCHLER (70) who has described a clone belonging to this group, from Java (Buitenzorg) and known as "Pisang Kladi". Since, as was pointed out in Part I, "Pisang" is the Malay word meaning banana and "Kladi" is the Sanscrit and subsequently Hindustani word of the same meaning, it seems very probable that this strain was introduced into Java from northern India, and hence probably arose among the twenty-four chromosomed races. I have been unable, to date, to obtain any information concerning it from Buitenzorg.

This completes our statement of fact and we must now turn to the interpretation of these facts.

PART IV.

Conclusions.

As has already been said (Part III) it has seemed best to consider eight as the basic chromosome number (diploid) in *Musa*, in spite of the fact that twelve is the lowest number actually found so far, and in spite

of the fact that all of the numbers so far available could be derived from twelve as a basis. This conclusion is based on the manner of grouping of the chromosomes at diakinesis in a number of the strains examined.

I have not myself been able to examine members of the sixteen chromosomed series but we may draw some conclusions from TISCHLER's (70) figures. If the basic number for *Musa* is eight, the chromosomes should according to the accepted view all pair uniformly at diakinesis, and there should be a perfectly regular meiotic figure. If, on the other hand, twelve is the basic number we should expect to find six good pairs and four unpaired chromosomes at diakinesis with a somewhat irregular meiotic figure. TISCHLER's figs. 21, 22 and 23, pl. XXXI (70) support the former conclusion. In the twenty-four chromosomed series also if twelve were the basic number, we should expect a perfectly regular pairing and an otherwise unmodified figure. Actually we do find this uniform pairing, showing that each chromosome has its homologue present, but instead of the diads being scattered uniformly over the surface of the nucleus, they are gathered into three groups of four each, a strong indication, as I believe, that four and not six is the basic haploid number. Moreover, the considerable degree of fertility of all of the twenty chromosomed races clearly indicate that they are euploid, which would not be the case if twelve were the basic diploid number. We may therefore take eight as our root and build upon this our geneological tree, hoping that eventually we shall find a strain, having that number. It is of course not impossible that this strain may lie outside the genus *Musa* (CLAUSEN, 19).

The first step which we may assume to have taken place in the phylogeny of the genus is the formation, doubtless under the influence of unusual external conditions, of functional diploid gametes, that is apospory in the formation of either male or female gametes or both. If such apospory took place in one parent only we would have as a result the union of a haploid with a diploid gamete, the zygote thus being triploid. In most cases, where they develop at all, such triploids (in this instance having twelve chromosomes), give sterile individuals although as was shown by BLACKBURN and HARRISON (9), this is not always the case. This fact would account for the rarity of triploids in the material available to me. More often, however, triploidy is followed immediately by a doubling of the chromosome number (ROSENBERG, 57; NAWASCHIN, 40), resulting in balanced hexaploids which are fertile. Such a doubling of the chromosome complement after hybridization has been observed in many plants and the resulting conditions are similar to those found in most of the hexaploid *Musas* of the *M. basjoo* series, which are highly fertile. It is probable, however, that such hexaploids as Lady FINGER and VIENTE COHOL (see Part II) have had a different origin, as we shall see later.

If, on the other hand, apospory occurred simultaneously in both parents, we would have the union of two diploid gametes, resulting in a tetraploid having sixteen chromosomes. We should expect no especial change from the parent type in such a tetraploid, unless it be in size. Since I have no information as to the nature of TISCHLER's clone "Dole" nor of any strain which might have given rise to it, the validity of this supposition can not at present be tested. Nor should we expect this number to double without further stimulus, since it is already balanced.

We now have two strains, one with sixteen chromosomes and one with twenty-four, both of them fertile, from which to develop the rest of our phylogenetic series in *Musa*. Since both strains bear more than two sets of homologues and both are derived from the same stock, we should expect them to be interfertile and by crossing, to give rise to a pentaploid series. Since this series would contain five complete sets of homologues, we would expect it to be fertile. The later in the evolution of the genus this cross was made the less definite would be the homology, but even if the two uniting strains had become quite divergent before the cross occurred, we would expect eight pairs of chromosomes at diakinesis and only four unpaired, so that our chance of obtaining a complete complement at the end of meiosis would still be high. Actually my observations of behaviour at diakinesis indicate the existence of at least nine and often all ten pairs, probably as a result of autosyndesis, so that the observed fertility of these races is not difficult to understand. It is possible too, that these pentaploid strains may also double to form some of the decaploid strains, though we have no definite evidence pointing to such an origin of the latter and we do have some evidence for quite a different origin.

The octoploid series is undoubtedly a complex. As we have already seen (Part II), the Gros Michel has probably arisen as a hexaploid-decaploid cross, and most of the octoploids whose pollen falls in Class D have probably been derived in the same way. This does not mean, however, that they are necessarily interrelated. On the contrary, they probably have arisen at various times as parallel lines. Such clones as Ta Ni Pa, and probably the Plantains as well, which have a fairly high pollen or egg fertility, seem more probably to have arisen by a doubling of the tetraploid. These clones would thus be true octoploids instead of hybrids. I have not been able to examine the meioses of Ta Ni Pa, but in Indio Plantain, which is to a certain degree fertile (not studied by COOPER, 21), all sixteen diads are formed at diakinesis and meiosis progresses regularly, evidence which supports the idea of a true octoploid constitution.

The material available to me has included only two septaploid strains, Dorado, which was obtained from Cuba and concerning whose real origin

we know nothing, and a hybrid clone of known origin. Theoretically the septaploid number could be derived as a hexaploid-octoploid cross, a pentaploid-nonoploid cross or a tetraploid-decaploid cross. Of these the first is by far the most probable and in our hybrid septaploid strain we have definite evidence of the feasibility of this type of cross. This strain is the progeny of a cross between Apple plantain (32) and Bastard Hemp (24) made under carefully controlled conditions¹. This cross has given us the expected number, twenty-eight. The specimen from which material was collected is recorded as resembling its pollen parent. Surprisingly this same cross has given rise to two other chromosome numbers. A second specimen is recorded as resembling the seed parent and has thirty-two chromosomes. This number is not theoretically possible in such a cross and suggests either that some foreign pollen had accidentally reached the stigma or else that apogamous propagation had taken place. The third example, "DUNLAP's Seedling" is of especial interest. It was not derived from a controlled cross, so that there is some possibility of error in identifying the male parent. However, since all strains of *Musa* in the neighborhood which might have served as pollen parent are known, we have very strong circumstantial evidence as to its origin. The seed parent was Apple Plantain (32) and the pollen parent was almost certainly Bastard Hemp (see Part III). The expected chromosome number in the progeny is therefore twenty-eight, This, however, did not prove to be the case, for the offspring showed distinctly forty chromosomes. This number can only be explained by assuming that twenty-four chromosomes had entered from the male parent. This is the diploid rather than the haploid number for Bastard Hemp. We are forced to conclude either (1) that dispermy had occurred, which seems unlikely or else (2) that a diploid, aposporously derived gamete from Bastard Hemp took part in the cross. The result recorded above is especially interesting since it shows us how one of our hypothetical parents of the Gros Michel might be synthesized. This synthetic decaploid is to a high degree fertile (Pollen Class A). It has already been successfully back crossed on MARTINI (24), another clone of the *Musa basjoo* (Bastard Hemp) series, but the seeds, although they possess good embryos, are without endosperm and hence sterile. It is to be hoped that some examples can be found possessing endosperm and capable of germination, as the resulting progeny should be of great interest.

There remain to be considered, among the *Eumusae*, the dodecaploid types which are evidently the result of doubling the hexaploid, and the nonoploid. In the latter, at reduction, all but four diads are formed and

¹ Mr. J. H. PERMAR has made to date some 30000 crosses at Almirante using various combinations. It is to be hoped that his results will be published at some future date.

divide normally. We are therefore led to believe that this strain is the result of crossing a true octoploid with a decaploid such as we have just considered. The sterility of this series is probably largely due, therefore, not to the presence of the four unpaired chromosomes, but to other unknown factors. TISCHLER (70) has already shown that contrary to our expectation, fertility in *Musa*, even in the balanced euploid series is roughly inversely proportionate to the chromosome number.

The subgenus *Physocaulis* is quite distinct from *Eumusa*, as we have seen (Part I). It seems probable that the number, twenty, which we find in *M. Ensete* is in no way connected with that of the pentaploid *M. textilis* group. Knowing as we do the great antiquity of the *Physocaulidae* (BERRY, 8, see Part I) it seems probable that they have been derived not from any forms existing today but from pre-tertiary ancestors. *Physocaulis* should itself be a very interesting group to study.

We have then the phylogenetic tree presented in fig. 127. Since it is based, for the most part, on the somatic numbers only, it can have only an hypothetical value and it should eventually be checked by a study of the reduction divisions in each of the fourteen chromosome groups established therein. The existence of these groups, however, cannot be questioned and the method by which they have been established is far less subject to error than a study of meioses alone would have been.

We have now gathered together a considerable mass of information concerning the material available to us for breeding purposes. What should be our program in the light of this knowledge? In Part I of this paper, we outlined two possible methods of attacking the breeding problem. According to the first method we would use Gros Michel as one parent in all crosses. For the other parent we would choose a thirty-two chromosomed, rarely-seeding variety, which is immune to the Panama disease. These requirements are filled by the ten plantains, by the Red and Green Red, by Kapas, Six A, the Congo and the Lacatan. The Red and Green Red are almost certainly gametically identical and the plantains carry only a single characteristic which we wish to incorporate in our progeny, namely, immunity. We can thus reduce the varieties to be utilized according to this method to seven; Gros Michel, Apple Plantain, Green Red, Kapas, Six A, Congo, and Lacatan. The remaining fifty-three clones of this series present in our collection are from our point of view of little or no interest as are the one hundred and one clones falling in other series.

If, on the other hand, we follow the second method of attack, that of attempting to obtain entirely new combinations of traits borne in distinct chromosome series, our material is quite different. These same six strains with the addition of Ta Ni Pa are desirable in our attempt to synthesize decaploids for future use as was done in the production of the

DUNLAP's Seedling. That such a synthesis is feasible has already been shown. The back cross of this synthetic strain on one of these seven should give us members of the nonoploid series, many of which, for example, Pisang Sri, today show very desirable features. All of the nonoploid series itself are useless for breeding purposes according to this

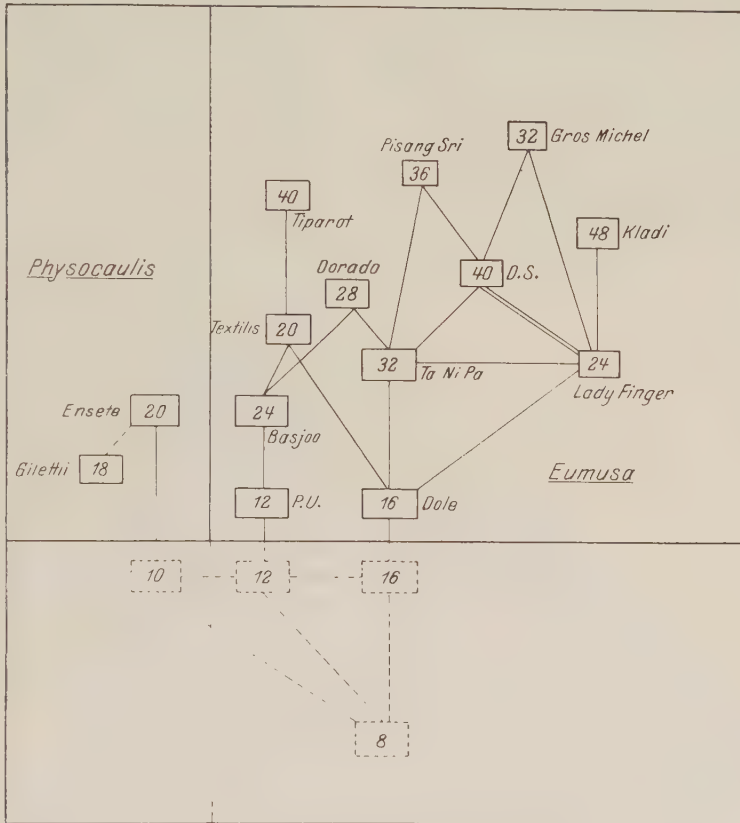
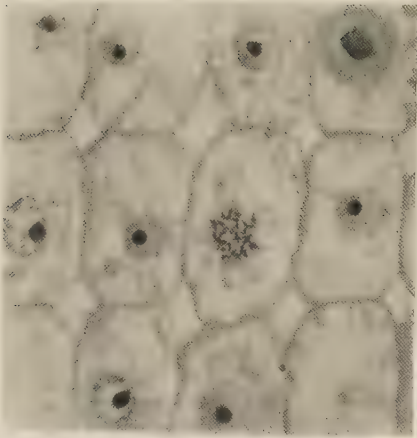
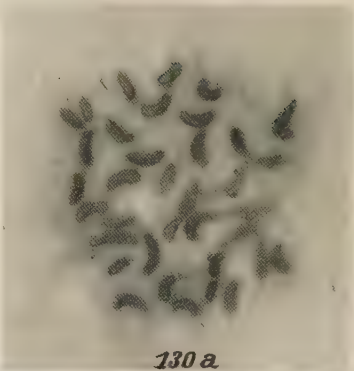


Fig. 127. Genealogical tree of the genus *Musa*.

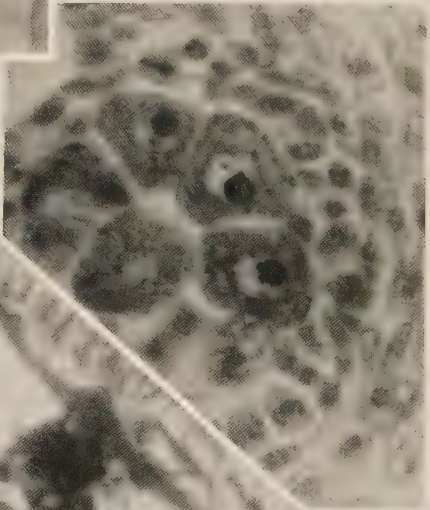
method, as are the triploids, tetraploids, pentaploids and septaploids. If the dodecaploid series were fertile it would be desirable, but since TISCHLER (70) has shown this series to be sterile, we must turn to the aposporous hexaploids for this element. All of the hexaploids from the Philippines with the exception of VIENTE COHOL and some of its allies are probably clones of *Musa basjoo*, and may be grouped under that head. *Musa seminifera*, *M. Clifortiana asperma*, *M. zebrina*, *M. sanguinea*, *M. rosacea*, and possibly, *M. acuminata* are probably too divergent from the commercial types to be of much value, and among the remaining



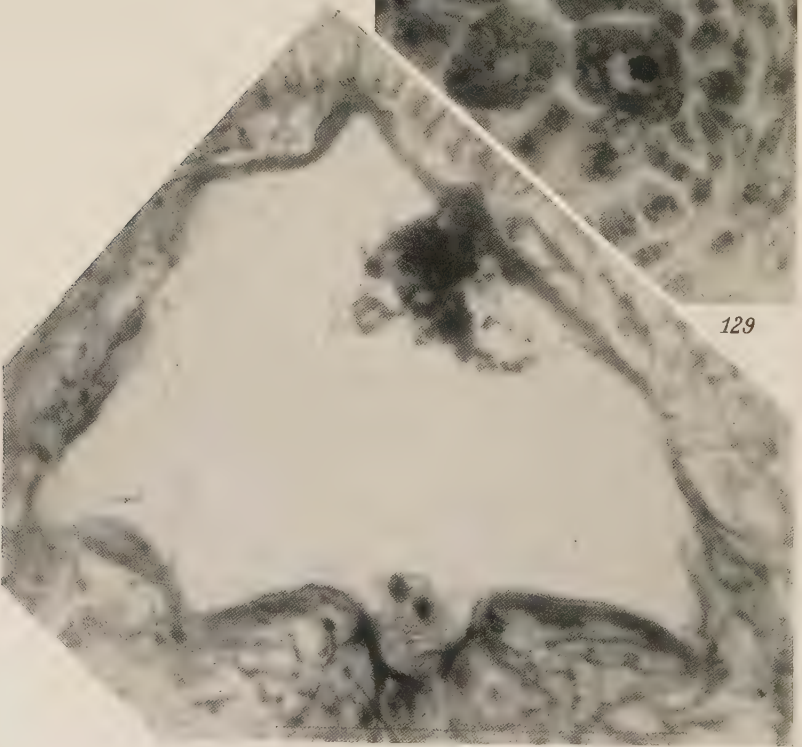
130



130 a



129



128

Fig. 128—130.

clones the five falling in pollen Class D, together with Martaban Dacca may be eliminated. We have left then Nandou Kababar (B), Pisang Kawahi (Tobelo and Galela), Lidi, Klui Kran, Lady Finger, Chek Pong Man Pluc, and Chuoi Cau Trang, and possibly Simiarum. In all probability Lidi and Klui Kran are clones of *Musa basjoo*. We have then in all six main hexaploid strains which should be crossed with our six octoploids in the hope of synthesizing new decaploids, and which should further be crossed with Tiparot, DUNLAP's Seedling and any decaploids which we may be able to obtain synthetically. As many seeds as possible should be germinated from each of these crosses and selections made from the progenies. Particularly attention should be paid to Lady Finger and VIENTE COHOL since they are fairly pollen-fertile and at the same time show today many desirable characteristics.

Such an indirect synthetic method may, to the uninitiated, appear far fetched. It has been argued that because only one Gros Michel has arisen in the twenty-five hundred years of recorded banana history, it is foolish to attempt to obtain another or a better one. But this is equivalent to telling a chemist that because we have no record of the existence of aurine before 1866, he should not attempt to synthesize it again. True, biology is not yet as exact a science as is the organic chemistry of today, but surely we have a better chance of obtaining what we want if we systematically cross types known to bear characters which we wish to combine, than if we sit back and wait for something to happen accidentally.

Literature cited.

1. d'Angremond, A.: Parthenokarpie und Samenbildung bei Bananen. Ber. d. dtsh. botan. Ges. **30**, 686—691. 1912. — 2. Parthenokarpie und Samenbildung bei Bananen. Flora **107**, 57—110. 1914. — 3. Avicenna: Avicennae medicorum Arabum principis, Liber canonis. Basileae, per Ioannes Hernagios. 1556. — 4. Baker, J. C.: Synopsis of the genera and species of the Museae. Ann. of Botany **7**, 189—222. 1893. — 5. Bally, W.: Die Godronschen Bastarde zwischen *Aegilops* und *Triticum*-Arten. Zeitschr. f. indukt. Abstammungs- u. Vererbungslehre. **20**, 176—239. 1919. — 6. Belling, J.: On counting chromosomes in pollen mother cells. Americ. Naturalist **55**, 573—574. 1921. — 7. Berry, E. W.: Contributions to the paleobotany of Peru, Bolivia and Chile. Johns Hopkins University Studies in Geology 1922. Nr. 4, 166. — 8. A Banana in the Tertiary of Colombia. Americ. Journ. of Science Ser. 5, **10**, 530—537. 1925. — 9. Blackburn, K. B. and Harrison, J. W. H.: The status of the British rose forms as determined by their cytological behaviour. Ann. of Botany **35**, 159—188. 1921. — 10. Blakeslee, A. F., Belling, J. and Farnham, M. E.: Chromosomal duplication and Mendelian phe-

Fig. 128. Embryo sac (Rodoc Clamp) showing polar nuclei and antipodals. See figure 41. $\times 675$. — Fig. 129. Cross section of anther (Gros Michel). See figures 66 and 67. $\times 675$. — Fig. 130. Cross section of root cortex (Chevalier) with nuclei in interphase (below center), prophase (center left), metaphase (center), and late telophase (upper right). Compare figure 121. $\times 675$. — Fig. 130 a. Detail from figure 130. $\times 3750$.

nomena in *Datura mutants*. Science **52**, 388—390. 1920. — 11. **Bonnet, Jean**: Recherches sur l'évolution des cellules-nourricières du Pollen, etc. Arch. f. Zellforsch. **7**, 604—722. 1912. — 12. **Brandes, E. W.**: Banana Wilt. Phytopathology **IX**, 9, 340—389. 1919. — 13. **Bruce, James**: Select specimens of Natural Hist. collected in Travels to discover the Source of the Nile in Egypt, Arabia, Abyssinia and Nubia. **5**, 36—41. Edinburgh: J. Ruthven 1790. — 14. **Buscalioni, L.**: Osservazioni e ricerche sulla cellula vegetale. Annuar real Istit. bot. Roma **7**, 253 bis 346. 1898. — 15. **de Candolle, A.**: Origine des plantes cultivées. Paris: G. Baillière 1883. — 16. **Catin, C. L.**: Recherches anatomiques sur l'embryon et la germination des Cannacées et des Musacées. Ann. d. sciences natur. botanique Sér. **IX**, 8, 113—146. 1908. — 17. Anatomie et développement de l'embryon chez les palmiers les Musacées et, les Cannacées. Cpt. rend. hebdom. des séances de l'acad. des sciences **146**, 938—940. 1908. — 18. **Chodat, R.**: La Chiasmotypie et la cinèse de maturation dans l'*Allium ursinum*. Bull. de la soc. botan. de Geneve 1925. 1—30. — 19. **Clausen, J.**: Chromosome Number and the Relationship of Species in the Genus *Viola*. Ann. of Botany **41** 676—714. 1927. — 20. **Cook, O. F.**: Food Plants of Ancient America, Ann. Rep. Smithsonian Institute. 1903. 481—497. — 21. **Cooper, G. P.**: Laboratory and Field Studies of the Pollens of some Varieties of *Musa*. Unpublished Miss. in the files of the U. F. Co. 1927. — 22. **Fawcett, W.**: The Banana. Its Cultivation, Distribution and Commercial Uses. Duckworth and Co., London 1921. — 23. **Garcillasso de la Vega**: Primera parte de los Commentarios reales. Madrid: Oficina real 1723. — 24. **Grant, Madison**: The passing of the Great Race. New York: Charles Scribners Sons 1916. — 25. **Greve, Gerhard**: Beiträge zur physiologischen Anatomie von *Musa Ensete*. Diss. Kiel 1909. — 26. **Griffiths, John**: The Paintings in the Buddhist cave temples of Ajanta, Khandesh, India. London 1896—97. — 27. **Hofmeister, W.**: Neue Beiträge zur Kenntnis der Embryobildung der Phanerogamen. II. Monokotyledonen. Abh. d. K. S. Ges. d. Wiss. VII. Leipzig 1861. — 28. **Humboldt, Alexander von**: Atlas géographique et physique du royaume de la Nouvelle Espagne. Paris 1811. — 29. **Humphrey, J. E.**: The development of the seed in the Scitamineae. Ann. of Botany **10**, 1—40. 1896. — 30. **Jaretsky, R.**: Die Degenerationserscheinungen in den Blüten von *Rumex flexuosus*. Forst. Jahrb. f. wiss. Botanik **LXVI**, 2, 301—319. 1926. — 31. **Kaufmann, B. P.**: The existence of double spiral bands and a "bouquet" stage in *Tradescantia pilosa* Lehm. (Preliminary note). Americ. Naturalist **59**, 110. 1925. — 32. **Lewitski, G. A.**: Die Bildung bivalenter Chromosomen in der Gonogenese von *Beta vulgaris* L. Planta **III**. 100—114. 1927. — 33. **Martius, Karl F. P.**: Beiträge zur Ethnographie und Sprachenkunde Amerikas, zumal Brasiliens. Leipzig: F. Fleischer 1867. — 34. **Megasthenes** (see Müller). — 35. **Michealis, P.**: Über den Einfluß der Kälte auf die Reduktionsteilung von *Epilobium*. Planta **1**, 569—582. 1926. — 36. **Mohammed**: The Koran. Trans. by George Sale (The Chandos Classics). Philadelphia: Scribner, Welford and Armstrong 1876. — 37. **de Mol, W. E.**: Duplication of generative nuclei by means of physiological stimuli and its significance. Genetics **5**, 225—273 (1923). — 38. **Morley** (Verbal statement to D. S. Johnson). — 39. **Müller, Karl et Theod.**: Fragmenta historicorum graecorum editore Ambrosio. Parisiis: Firmin Didot 1848—1874. — 40. **Nawaschin, M.**: Über die Veränderung von Zahl und Form der Chromosomen infolge der Hybridization. Zeitschr. f. Zellforsch. u. mikroskop. Anat. **6**, H. 1 u. 2, 195—233. 1927. — 41. **Němec, B.**: Das Problem der Befruchtungsvorgänge und andere zytologische Fragen. Berlin 1908. — 42. **Noll, F.**: Über Fruchtbildung ohne vorausgegangene Bestäubung (Parthenokarpie) bei der Gurke. Ber. d. Niederrhein. Ges. f. Natur- u. Heilk. Bonn 1902. — 43. **da Orta, Garcia**: Coloquios dos simples e drogas he cousas medicinais da India compostos pello Doutor Garcia da Orta. Goa: Johannes de Endem 1563. — 44. **Oviedo y Val-**

- des, **Gonzales Fernandez de**: Historia general y natural de las Indias, Islas y Tierra-Firme del Mar Oceano. 1, 290—293. Imprenta de la real Academia de la Historia. Madrid 1851—1855. — 45. **Peterson, O. G.**: Musaceae (in: Die natürlichen Pflanzenfamilien. Engler, A. und Prantl, K.). II. Teil, 6. Abt. Leipzig 1889. — 46. **Pfeffer W.**: Pflanzenphysiologie. 2. Aufl. Leipzig 1897. — 47. **Pickering, Charles**: A Chronological History of Plants. Boston: Little, Brown and Co. 1879. — 48. **Pliny, C. Plinii**: Naturalis Historia XII, 2—6 (6—13), 217. D. Detlefsen. recensuit, Berolini. Apud Weidmannos 1866. — 49. **Popenoe, W.**: Letters in the files of the U. F. Co. Boston. — 50. **Prescott, W. H.**: History of the conquest of Peru. New York: Harper and Brothers 1847. — 51. **Quisumbing y Arguellas, Eduardo**: Studies of Philippine bananas. Philippine agricultural review 12, Nr. 3. 1—96 1919 — 52. **Reinhardt, L.**: Kulturgeschichte der Nutzpflanzen (1. Hälfte). 192. Munich 1911. — 53. **Reinking, Otto** (see Reynolds 54, 15). — 54. **Reynolds, P. K.**: The Banana, Its History, Cultivation and Place among Staple Foods. Boston and New York: Houghton, Mifflin Company 1927. — 55. **Rosenberg, O.**: Cytologische und morphologische Studien an *Drosera longifolia* × *D. rotundifolia*. Kgl. Svensk. Vet. Handl. 43, 3—64. 1909. — 56. Die Reduktionsteilung und ihre Degeneration in *Hieracium*. Svensk. Botan. Tidskr. 11, 145—206. 1917. — 57. Die Semiheterotypische Teilung und ihre Bedeutung für die Entstehung verdoppelter Chromosomenzahlen. Hereditas 8, 306—338. 1926. — 58. **Sagot, P.**: Bananier Fehi, sa forme asperme et sa forme seminifère. Bull. de la soc. botan. de France 33, 317—326. 1886. — 59. **Sax, K.**: Sterility in wheat hybrids. II. Chromosome behaviour in partially sterile hybrids. Genetics 7, 513—552. 1922. — 60. **Schumann, K.**: Musaceae. Das Pflanzenreich (Engler, A.) 4, 45, H. I, 1—45. 1900. — 61. **Serapiam**: Liber Serapionis aggregatus in medicinis simplicibus. Mediolani, folio 1475. — 62. **Sharp, L. W.**: An Introduction to Cytology. New York: McGraw Hill Book Co. 1926. — 63. **Shreve, F.**: The development and anatomy of *Sarracenia purpurea*. Botan. Gaz. 42, 107—126. 1906. — 64. **Stout, A. B.**: The individuality of the chromosomes and their serial arrangement in *Carex aquatilis*. Arch. f. Zellforsch. 9, 114—140. 1913. — 65. **Strasburger, E.**: Über Polyembryonie. Jenaische Zeitschr. f. Naturwiss. 12, 647—660. 1878. — 66. **Täckholm, G.**: Zytologische Studien über die Gattung *Rosa*. Acta Horti Bergiani 7, 97—381. 1922. — 67. **Taylor, W. R.**: The smear method for plant cytology. Botan. Gaz. 78, 236 bis 238. 1924. — 68. **Teodoro, U. S.**: A preliminary study of Philippine bananas. Philippine Journ. of Science 10, 379—421. 1915. — 69. **Theophrastus**: Enquiry into plants I, IV, IV, 4—5, p. 315. Loeb Classical Library. New York: G. P. Putnam's Sons 1923. — 70. **Tischler, G.**: Untersuchungen über die Entwicklung des Bananen-Pollens, I. Arch. f. Zellforsch. 5, 622—670. 1910. — 71. Über die Entwicklung der Samenanlagen in parthenokarpen Angiospermen Früchten. Jahrb. f. wiss. Botanik 52, 1—84. 1912. — 72. Die Periplasmodiumbildung in den Antheren der Commelinaceen und Ausblicke auf das Verhalten der Tapetenzellen in den übrigen Monokotylen. Ebenda 55, 53—90. 1915. — 73. Allgemeine Pflanzenkaryologie. K. Linsbauer, Handbuch der Pflanzenanatomie 2. Berlin 1921—1922. — 74. **Unger, F. J. A. U.**: On the principal plants used as food by man. U. S. Pat. Office rep't 1859. — 75. **Watt, George**: A dictionary of the economic products of India. London: W. H. Allen and Co. 1889—1896. — 76. **Wittmack, L.**: *Musa Ensete*. Ein Beitrag zur Kenntnis der Bananen. Diss. Kiel 1867.

VITA.

PHILIP R(ODNEY) WHITE, son of HENRY K(IRKE) and MARY P(ATTEE) WHITE, was born in Chicago, Illinois, July 25, 1901, graduated from Post Creek High School, Missoula County, Montana in 1918, received A. B., U. of Montana, 1922, was Teaching Fellow, U. of Washington, 1922—'23 and Lecteur d'Anglais, École Normale d'Instituteurs, Valence, Drôme, France, 1923—'24. He visited Italy and Switzerland in the spring of 1924. He entered the Johns Hopkins University as graduate student and Assistant in Botany in October 1924, was Assistant in Botany, 1925—'26 and Microscopic Technician, U. S. Bureau of Plant Industry 1925—'26. He was a member of the Johns Hopkins Botanical Expedition to Jamaica in the summer of 1926, and attended the International Botanical Congress, Ithaca, N. Y., August 1926. He was special investigator for the United Fruit Company, 1926—'28, working in Jamaica, in Baltimore and at Almirante, Panama, visiting Costa Rica and Cuba at this time.

Publications: Studies in the Physiological Anatomy of the Strawberry.